



THE SEASIDE SPARROW, ITS BIOLOGY AND MANAGEMENT



Edited by
THOMAS L. QUAY
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Occasional Papers of the
North Carolina Biological Survey
1983-5

**Proceedings of a Symposium
Held at Raleigh, North Carolina
1-2 October 1981**



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ELOISE F. POTTER

Editor

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and the United States Fish and Wildlife Service**

FRONTISPIECE:
THE NINE RACES OF THE SEASIDE SPARROW
Watercolor by John Henry Dick

NIGRESCENS

PENINSULAE

SENNETTI

NIGRESCENS
JUV.

FISHERI

PELONOTA

MIRABILIS

MACGILLIVRAII


MARITIMA

JUNCICOLA

MARITIMA
IMM.

THE NINE RACES OF THE
SEASIDE SPARROW
AMMOSPIZA MARITIMA

John H. Dick '81



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INTRODUCTION

Imagine for a moment you are on the Eastern Shore of Maryland. Far to the west is a low horizon of Loblolly Pines, indicating the limits of the sandy loam soils of the coastal plain. In all other directions is marsh, and except for the two-lane road that extends for 10 miles and connects Deal Island with the forested mainland of the Delmarva Peninsula, there is no place in view that is more than a few inches above the reach of high tide. A rich green expanse of windswept cordgrasses is irregularly broken by dark islands of Black Needlerush, and here and there, slightly higher parts of the marsh are claimed by an unmappable maze of tidal creeks that twice daily flood the low marsh with brackish water. Here there is no protective overstory; only grasses emerge from a world that at one hour belongs to the harsh extremes of the sun and at another to the sea. This inhospitable place is the home of the Seaside Sparrow. Seasides, and other salt-marsh dwellers, live here under the terms of a genetically signed contract with the marsh, and their daily activities are dictated by an oddly synchronized cadence of the salt-laden tides.

The May morning songs of Red-winged Blackbirds come from every direction, and sporadic outbursts of loud Clapper Rail clucks are heard from deep within the salt meadows. The voices of counter-dueling Long-billed Marsh Wrens and the high, faint trills of Sharp-tailed Sparrows would be hard to miss by those attuned to such things. The one voice that in my mind characterizes the salt marsh, however, is the song of the Seaside Sparrow. It is not a strong song, nor does it possess any musical complexity that makes one wish to remember it. The weak introductory notes, followed by a buzzy trill, might be what a miniature Red-winged Blackbird would sound like if it were singing in a paper bag. Nevertheless, once this song is recognized, you soon become aware that the sound of vocalizing Seaside Sparrows permeates the marsh. Their songs come from everywhere, and the number of little brown birds perched on grasses throughout the meadow makes you aware that the marsh is indeed rich in life. The avian diversity of salt marshes is seldom as low as it seems on casual inspection, but the number of species that regularly nest in these habitats is quickly tallied. In addition to the birds mentioned above, only ducks, herons,

Willetts, Common Yellowthroats, and several other species of rails regularly frequent the marsh; as far south as the eastern shore of Maryland, at least, Marsh Hawks occasionally nest locally. What the breeding-bird fauna lacks in variety, however, is more than made up for in numbers. The productivity of salt marshes is well documented, so it comes as no surprise that birds congregate here in numbers. Density estimates of nearly 2,000 breeding male Seaside Sparrows per square kilometer have been reported. Although this density seems to be somewhat high, it does exemplify how abundant these sparrows may be in ideal habitat.

My introduction to the Seaside Sparrow was in Zoology-406, when the instructor, John Funderburg, explained to the ornithology class the complex zoogeographic evolutionary history of this species. I was impressed and soon became captivated with ideas about effects of changing Pleistocene shorelines on other animal groups. Not until coming to work at this museum did I realize that what I had heard years before was the yet unpublished research of Funderburg and Tom Quay. Years after Zoology-406, while on the staff of the Florida State Museum, I had the opportunity to join Bill Hardy in recording the voices of both the Dusky Seaside and Cape Sable Sparrows. Seeing on successive days the two extreme color phases of this bird triggered my memory of Funderburg's class lecture, and gave me the incentive to record and observe additional races and populations of Seasides. Travels from Delaware to Louisiana allowed me to witness not only the variety of voices and birds, but also the differences in floristic composition of the marshes and the variations in their sparrow populations. During these travels I inquired of nesting localities from others who were studying the species, and heard of yet others, and from this field work grew the idea of this symposium. Not only would a symposium allow us to collect current research and put it into perspective, it also would provide the incentive for Funderburg and Quay to finally publish their long overdue treatise on Seaside Sparrows evolution.

Even for sparrows, *Ammodramus maritima* is an inconspicuous little bird. Its distribution is restricted and its habitat monotonous. Yet, it was this confined geographic and ecological distribution that allowed rapid genetic differentiation and development of spe-

cialized behavioral and physiological profiles in the species. The Seaside Sparrow is one of the few song birds that can survive in uninterrupted salt marshes and, except for the Clapper Rail, is the only North American bird essentially restricted to these habitats. The early recognition of different kinds of Seaside Sparrows elicited much taxonomic attention. The geographic lineup of light and dark races added elements of curiosity and confusion, which in turn provided long-term support for the idea that several species were represented in this complex. Meanwhile, expanding interest in bird watching and species life lists, paralleling a time of growing concern for preserving species and conserving wetlands, supplied additional attention to the named and depleted population segments of these sparrows. The concept that the bird is an excellent indicator species for gauging the overall health of salt-marsh communities is long overdue.

Ornithologists, it seems, have converged from diverse interest perspectives to interpret the nature of Seaside Sparrows—taxonomy, ecology and behavior, and preservation. Although these areas of interest did not develop simultaneously, they are not mutually exclusive. We have assembled for this symposium nearly all workers currently involved with Seaside Sparrow research. They have come not only from different parts of the country, but from different generations and schools of thought. What follows is not simply a report on the Seaside Sparrow from throughout its total range, but a series of serious attempts to understand various aspects of the bird's biology. Those of us who attended the October 1981 Symposium gained much insight into the nature of *Ammospiza maritima*, and even into the political and social issues impacting on the species. We hope this publication will provide a base document to stimulate and complement future studies of this non-descript, and most appropriately named, little bird.

About the 1981 Symposium:

Held in Raleigh, North Carolina, on 1 and 2 October 1981, the Seaside Sparrow symposium was sponsored jointly by the North Carolina Biological Survey and the U.S. Fish and Wildlife Service. About 75 invited participants attended the three major sessions.

The opening session, which I moderated, provided an overview of the bird and its habitat. John B. Funderburg Jr., Director of the North Carolina State Museum of Natural History, welcomed the participants and introduced the keynote speaker, F. Eugene Hester, then Acting Deputy Director of the U.S. Fish and Wildlife Service. Hester's address was followed by three papers and a panel discussion. Panelists were Lee (moderator), Funderburg, Hester, Thomas L. Quay, Oliver L. Austin Jr., Arthur W. Cooper, and Chandler S. Robbins.

The second session, moderated by Chandler S. Robbins, USFWS, addressed specific aspects of the biology of the Seaside Sparrow. The third session, which focused on the protection and management of this sparrow, was moderated by James F. Parnell, of the University of North Carolina at Wilmington. The three papers sessions correspond to Parts I, II, and III in this publication of the proceedings of the symposium.

A brief question-and-answer period followed each presentation. These informal exchanges and the panel discussion were recorded, and the tapes and unedited transcripts are on file at the State Museum. However, publication of the discussion was deemed unnecessary because authors revised their papers in response to questions raised from the floor.

Several acknowledgments seem in order. The North Carolina Natural History Society, a support group for the State Museum, and the Carolina Bird Club covered the expenses for the coffee breaks. Cynthia Wilkenson and Kaye Cross handled most of the work involved with registration. Steve Platania and Mary Kay Clark were responsible for the audio-visual portions of the program.

The original painting contributed by John Henry Dick as a frontispiece for this publication and the master tape recording provided by Bill Hardy for production of the record that accompanies this publication deserve far more than a simple acknowledgment. To say that these men responded quickly and generously to my requests for their professional assistance is an understatement. The finished products were in my office long before the opening session of the symposium. The birds depicted in the painting, incidentally, were hand-picked by Oliver L. Austin Jr. from the collection at the Florida State Museum, as typical representatives of each race. Paul W. Sykes Jr. provided the photograph of the Dusky Seaside Sparrow that appears on the front cover.

On Thursday evening, following the first papers session, a social was held at my home. Here participants were able to share information that was not formally presented, particularly in regard to the maintenance of captive birds. The sponsors like to think that this symposium had direct, immediate, and beneficial effects on the sparrow itself. A free exchange of thoughts took place between researchers concerned for the welfare of certain Seaside Sparrow populations and government officials legally responsible for carrying out the provisions of the Endangered Species Act. Although the future of the now totally captive population of Dusky Seaside Sparrows looks bleak, at least concerted efforts are being made in behalf of these birds. See *Florida Naturalist* 55(5):16 for the most recent information presently available on government policy regarding the Dusksies and on private sponsorship of the captive-breeding program.

Publication of the "34th Supplement to the American Ornithologists' Union Check-list of North American Birds" (Auk 99:1-16CC) in July 1982 moved the Seaside Sparrow from the genus *Ammospiza* to *Ammodramus* and changed the common names of the Marsh Hawk, Everglade Kite, and Long-billed Marsh Wren. Because much of the type had already been set when this supplement appeared, the editors decided to retain the common and scientific names in use at the time the symposium took place.

In closing, I thank all who contributed to the success of this symposium. The editors are somewhat embarrassed by the time lag between presentation of the papers and their publication. Those who have worked closely with us are aware of the unexpected circumstances responsible for the delay. Your patience is appreciated.

DAVID S. LEE

North Carolina Biological Survey
North Carolina State Museum
of Natural History

Raleigh, North Carolina
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PART I
The Seaside Sparrow:
An Overview

KEYNOTE ADDRESS

F. EUGENE HESTER
Acting Deputy Director
U.S. Fish and Wildlife Service
Washington, D.C.

I am happy to be here today to open this symposium and, hopefully, to facilitate its success. There are several reasons why I am glad to be here.

For one thing, I think this symposium had its roots, at least in part, in plans for a special day in honor of T. L. Quay upon conclusion of his highly successful career in ornithology, and zoology in general, at North Carolina State University. That was over a year ago. John Funderburg, Jim Parnell, and others, including myself, had envisioned a day of scientific discussion followed by some roasting and a dinner. There was only one problem. Dr. Quay would have no part of it. Apparently, it had something to do with the fact that he wasn't retiring; he was just making a change in employment by starting to work for the Museum.

There was a little story I wanted to tell at that occasion and, to keep this session from getting too serious, maybe I should tell it now.

When I first went to North Carolina State University 30 years ago, I, frankly, didn't know there was such a thing as a Seaside Sparrow. But soon I heard Tom telling of his trips to the coast and about the various studies he had made. It was along about that time that Tom was preparing a fairly major manuscript on "An Ecological Study of the Seaside Sparrow." Apparently, I wasn't the only one naive about the Seaside Sparrow, because when Tom's prized, handwritten manuscript first came back from the typist, his enthusiasm quickly sank: There, on all 56 pages of the text, it had been identified as the "seasick" sparrow.

In addition to honoring Dr. Quay, I am glad to be here for other reasons. For one thing, the U.S. Fish and Wildlife Service is concerned with maintaining and restoring endangered species and with preservation of sensitive habitats. Thus, you and we share some strong common interests.

I am not here today as a specialist on the Seaside Sparrow (or seasick sparrow either). You are the authorities on that . . . from speciation to habitat requirements. But I think I can contribute to this session by explaining the legal authorities conveyed by the Endangered Species Act, and I can explain our interpretation and imple-

mentation of those authorities. This symposium also provides me an opportunity to explain the reasoning behind some of the decisions of the Service relative to some of your interests, recommendations, and concerns.

I realize that some of your ideas and approaches as to how to accomplish important goals may be different from ours. But before we get into those differences, I would like to comment about several things on which we are in agreement.

I believe we are all appropriately concerned and active about maintaining sensitive wildlife habitat. Estuarine and riverine areas are some of the most sensitive of habitats . . . both in terms of fragility and in terms of pressures for change. Such areas are frequently proposed for modification . . . whether to deposit dredge spoil, fill in a wetland for a summer home, or drain a marsh for mosquito control. Our Ecological Services biologists, carrying out the responsibilities of the Fish and Wildlife Coordination Act, the Clean Water Act, and several other acts, evaluate the ecological impact of the proposed changes and work to minimize impact. We also preserve some habitat as part of our National Wildlife Refuge System. I know that you are also actively involved in making your own input into decisions about preserving habitat.

And when it comes to saving endangered species, you and we are concerned with that, too. I suspect I don't have to tell this group about the Whooping Crane, Puerto Rican Parrot, Bald Eagle, Everglade Kite, or dozens of others. Most have been real success stories, and some species have returned from the very brink of extinction. Some, such as the American Alligator in Louisiana, have responded to sound management and have increased in abundance to the point that they are no longer either endangered or threatened. Others, like the California Condor, may be too far gone already. But we have joined with the National Audubon Society and others to do what we can, even against inevitably difficult odds against success.

My point is that saving habitat and saving species is very important, and it is something in which you and we share a common interest and commitment. Why, then,

are we not in total agreement about what needs to be done and how to go about it? Why do some communications with you seem to convey a stand-offish attitude and sometimes a lack of commitment to an all-out effort to save animals such as the Seaside Sparrow?

For one thing, no agency has *carte blanche* authority to carry out the things it would like to do. All Congressional mandates have limitations on them. Either they were originally passed with those limitations or they are incorporated through amendments. The mandates also may be administratively limited by policy decisions of the administering agency. In addition to legal and policy limitations, there are always financial limitations.

Under the Fish and Wildlife Coordination Act and the Clean Water Act, for example, we are advisory to the Corps of Engineers or other agencies by providing ecological evaluations of their projects and their proposed permits. And even authorities as tough and uncompromising as the Endangered Species Act, which we administer, must be carried out with adequate concern for the broad interests of the Nation.

Another consideration has to relate to priorities. Every agency must face this as there is never enough money or manpower to do all that needs to be done. When some things get done, others don't get done.

From all these considerations has come our position relative to our authorities and how we will implement them. Some that are pertinent to this symposium are these:

- Our overall objective is to facilitate the growth and development of the Nation while preserving the environment.
- For most species (but not for endangered species), we have developed habitat-evaluation procedures to facilitate mitigation. Through improvement of remaining habitat, loss of some habitat can often times be offset.

- We will manage our National Wildlife Refuge lands primarily for the benefit of fish and wildlife. In so doing, however, we must always be aware that when we manage for some species, we manage against others.
- We manage our refuge system so as to be reasonably in concert with the needs off the refuge. This might best be thought of as being good neighbors and involves such things as passage of storm waters through refuge areas, suppression of wildfires, and control of noxious plants and animals, including mosquitoes.
- For endangered species, our objective is to increase their abundance to the point they are no longer threatened or endangered.
- We place greatest emphasis on preserving animals in their original habitat and less emphasis on establishing them in areas where they did not previously exist.
- We place greater emphasis on preserving populations than on subpopulations and greater emphasis on species than on subspecies. Hybrids have no status as endangered species.

The U.S. Fish and Wildlife Service is glad to be a co-sponsor of this symposium, along with the North Carolina State Museum and the N.C. Biological Survey. This symposium provides a meaningful forum for the presentation of information, concepts, and ideas. Obviously, it facilitates the presentation and discussion of biological information. It is my hope that it will go beyond that by facilitating a meaningful discussion of the biological, political, and administrative information that in total shape the future for all species.

I share your deep interest and concern about the Seaside Sparrow and other endangered species. I look forward to this opportunity to discuss these matters with you.

The Salt-marsh Ecosystem

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Abstract. Salt marshes are stands dominated by grasses and rushes rooted in the intertidal zone, which are alternately flooded and exposed by the tide. Generally three zones can be recognized in a salt marsh: a zone regularly flooded by the tide, a zone above normal high tide irregularly flooded by tides, and a zone at the edge of the upland. In the range of the Seaside Sparrow, there are five types of salt marsh. Marshes from New England to New Jersey typically have a broad zone of *Spartina patens* (Ait.) Muhl. above the normal tide line where peat accumulates, a zone of *Spartina alterniflora* Loisel. of variable width, and *Juncus gerardi* Loisel. at higher elevations. A similar pattern occurs between New Jersey and northern North Carolina except that *Juncus roemerianus* Scheele, *Spartina cynosuroides* (L.) Roth, and *Scirpus robustus* Pursh, all southern species, occur here. Along the southeastern Atlantic Coast vast stands of *Spartina alterniflora* occur on soft, silty sediments in the extensive intertidal zone. *Juncus roemerianus*, *Spartina patens*, and *Distichlis spicata* (L.) Greene dominate the zone above normal high tide. In Florida, mangroves and several other southern species occur as far north as St. Augustine. Extensive bodies of dry salt marsh occur throughout Florida and in the Everglades. Along the Gulf Coast, species composition is similar to that along the southeastern Atlantic Coast. However, *Juncus roemerianus* occurs in larger pure stands. Salt marshes disappear in southwest Texas where high temperatures and low rainfall produce hypersaline conditions. Salt marshes are generally considered to be important contributors, through the export of organic matter, to the high productivity of estuarine systems. This phenomenon is thought to be a major cause of high production of fish and shellfish in East and Gulf Coast estuaries and near-shore ocean waters, a view that has recently been questioned. Man has numerous impacts on salt marshes. The most detrimental of these stem from dredging and filling and Salt-marsh Mosquito control.

The salt marshes that form the habitat for the Seaside Sparrow (*Ammospiza maritima*) are stands of grasses and rushes rooted in the intertidal zone, which are alternately flooded and exposed by the rise and fall of the tide. Salt marshes typically are interlaced with a network of dendritic tidal creeks through which water, nutrients, organic matter, plankton, fish, and shellfish move with the tides. Such marshes and their immediately adjacent waters are parts of a system of food chains and nutrient cycles, and form one major component of the vast estuarine system (Cooper 1974) of the East and Gulf Coasts of the United States.

The adjectives used to describe a typical salt marsh—open, vast expanse, grassland, absence of trees—are also adjectives that describe the habitat of the Seaside Sparrow. This fascinating little bird has clearly evolved in, and is adapted to, the salt marshes of the middle and southeastern Atlantic and Gulf Coasts of the United States, and its ecology is intimately influenced by that of the marshes in which it occurs.

Structurally, salt marshes are typical grasslands, consisting of extensive stands of several species of

grasses or rushes of similar stature and growth form. Three general zones can be recognized in every marsh. The first is a portion that is regularly flooded by lunar tides. Here, because the tides remove organic debris, the soil surface is generally bare of accumulated organic matter, although algal blooms and extensive animal populations regularly occur on the surface. This zone may be extensive, as in southeastern marshes, or may be a very narrow fringe along the edge of tidal creeks. A second region, lying above the normal high-tide line, is flooded irregularly by wind and storm tides. Organic matter typically accumulates here, frequently in the form of peat. Finally, there is a zone where the marsh and the adjacent upland come into contact. Shrubs are common here as are tall aquatic graminoids and sedges where freshwater seepage and accumulation occur.

Certain features of the intertidal environment are crucial in determining plant and animal distribution in salt marshes. Most critical of these are interactions of tides with the elevation of the land surface and differences in salinity that can largely be related to these interactions. The distribution of the major salt-marsh

plant species is determined primarily by the depth and duration of tidal flooding, and its consequent effects on substratum aeration, and by salinity of the substratum, which can be increased above the general levels of the flooding sea water by evaporation or reduced below it by rainfall. In addition to these primary habitat factors, other variables such as the oxygen content of the substratum and variations in its ionic composition, particularly with respect to plant nutrients, may be important.

A small number of plant species dominate East and Gulf Coast salt marshes. *Spartina alterniflora* Loisel., which manifests considerable variation in height, is the major species of the intertidal zone. *Distichlis spicata* (L.) Greene and *Salicornia* sp. commonly occur at or slightly above the normal high-tide line. *Spartina patens* (Ait.) Muhl. and two species of *Juncus*, *J. gerardi* Loisel. in the north and *J. roemerianus* Scheele in the south and Gulf Coast, are the dominants of the zone that is irregularly flooded by tides. *Scirpus* sp., *Typha* sp., and other freshwater aquatic species are common in the upper elevations of most salt marshes.

Salt Marshes of the East and Gulf Coast

In the range of the Seaside Sparrow, from southern Massachusetts to the Gulf Coast of Texas, there are five types of salt marsh. These are marshes occurring: (1) in New England and New Jersey; (2) from southern New Jersey, the eastern shore of Maryland, and Virginia to the Pamlico Sound region of North Carolina; (3) along the southeastern Atlantic Coast from North Carolina (Cape Lookout) to the vicinity of Jacksonville, Florida; (4) on the peninsula of Florida; and (5) along the Gulf Coast from Florida to Texas. Although there are some plant species that occur throughout all of these regions (*Sp. alterniflora*, *D. spicata*), others are more local in distribution and the marshes of each region are characterized by unique combinations of dominant plants and habitat conditions. Thus, the marshes so produced, although generally similar in structure and physiognomy, offer slightly different combinations of niches, which the various taxa of Seaside Sparrows exploit.

1. New England to New Jersey: The salt marshes of southern New England and New Jersey actually occur as far north as the Bay of Fundy. Zonation is clear-cut (Nichols 1920, Chapman 1940, Miller and Egler 1950, Niering 1966, Redfield 1965). The substratum in these marshes is peaty or semipeaty, particularly in areas near or above high tide. Pure stands of *Sp. alterniflora* occupy the intertidal zone, occurring as narrow fringes along creeks where elevation gradients are steep or in larger areas where slopes are more gentle. A well-developed zone of *Sp. patens* and *D. spicata* always occurs above the intertidal zone. These vast meadows were the source of salt hay, so extensively collected by early New Englanders. Pure stands of *J. gerardi* form in the higher parts of the zone above normal high tides, frequently composing a fringe at the edge of the upland. Pannes (bare areas) are scattered throughout the upper marsh. These typically support small individuals of *D. spicata*, *Sp. alterniflora*, and *Salicornia* sp. There is usually a narrow belt of *Panicum virgatum* L. and *Spartina pectinata* Link, with numerous other species, at the very edge of the upland. Similar patterns occur in Long Island (Conard 1924, Conard

and Galligar 1929, Taylor 1938), except that the proportion of *Sp. patens* is frequently very large with *Sp. alterniflora* covering a small fraction of the total area.

2. New Jersey to northern North Carolina: The area between New Jersey and Pamlico Sound in North Carolina is a broad zone of transition between the New England marshes and those more characteristic of the southeastern Atlantic coastal plain. Here, again, *Sp. alterniflora* is relatively limited, and the greatest area of the marsh is typically covered with *Sp. patens* (Snow 1902, Harshberger 1909, Fender 1938, Martin 1959). The barrier islands of Virginia, where vast stands of *Sp. alterniflora* occupy the area between the narrow beach fringes and the mainland of the Delmarva peninsula, are an exception to the general pattern. Several southern species first occur in this region. *Spartina cynosuroides* (L.) Roth and *Scirpus robustus* Pursh both occur along creeks in Delaware Bay (Chamberlain 1951) and *J. roemerianus*, found near the mouth of the Potomac and at Ocean City in small quantities, increases in importance toward the mouth of Chesapeake Bay. *Juncus gerardi* also occurs in the area, again as a typical fringe above *Sp. patens* at the marsh border. The western shore of Chesapeake Bay is strongly influenced by fresh water (Shreve 1910). *Spartina alterniflora* occurs along streams influenced by tides but is replaced by *Sp. cynosuroides* upstream where the flooding water is less saline. Other freshwater species, such as *Scirpus olneyi* Gray, *Sc. robustus*, and *Typha* sp. are common in areas with low salinities. These species, plus *Cladium jamaicense* Crantz and *J. roemerianus* form vast stands of nearly freshwater marsh in Currituck Sound in extreme northeastern coastal North Carolina. This area was much more saline in the early 1900s but has become progressively fresher because of the closure of several inlets in Currituck Banks and because no major hurricanes have occurred since the late 1950s.

3. Southeastern Atlantic Coast: From the Cape Lookout region of Pamlico Sound, North Carolina, south to Jacksonville, Florida, vast expanses of salt marsh occur. These form in estuaries where major rivers, draining huge expanses of the piedmont and coastal plain, deposit heavy silt burdens (Linton 1968). These marshes are best developed from Cape Fear, North Carolina, south to northern Florida, and are often called *regularly flooded* because they are flooded twice daily by lunar tides. Marshes also form behind the barrier islands that create Pamlico Sound and on the sound's inner fringes and up its tributary rivers as far as there is an influence of salt water. Tidal flooding in these marshes is wind-driven, and they are consequently referred to as *irregularly flooded* marshes. Tidal amplitudes are usually less than a foot, but may be much greater when storms or major fronts cause rapid changes in wind velocity.

The characteristic feature of the regularly flooded, or low, salt marshes is the vast expanse of *Sp. alterniflora* covering the soft, gray, silty sediments lying between mean sea level and mean high water. Intricate, dendritic creek patterns, associated with high tidal amplitudes and the slow, gentle subsidence of the coastal plain, permeate these vast expanses of grass. Tidal

amplitudes vary from 2 to 5 feet in North Carolina to over 8 feet in South Carolina and Georgia. Several distinct community types, based on combinations of physiographic and biotic factors, occur (Adams 1963). There is a zone of very soft, gray silt along the creek banks below the level of vascular plants. These bare sediments are populated by growths of algae, chiefly diatoms. *Spartina alterniflora* grows along the creek banks, from approximately mean sea level to the crest of the raised levee. Here it reaches its greatest height, averaging from 4 to 8 or 10 feet tall. On the top of the natural levee occurring along the creeks, *Sp. alterniflora* of medium height (2-4 ft) occurs. Away from the streams *Sp. alterniflora* decreases to less than a foot in height in the extreme upper part of the intertidal zone. This zone of short *Sp. alterniflora* usually covers 50% or more of the surface area of the marsh. Its substratum is much firmer than that of the tall and medium *Spartina* zones, owing both to a denser network of roots and rhizomes and to a greater sand content. *Salicornia* sp. and *Limonium carolinianum* (Walt.) Britt. are frequently mixed with short *Spartina* in sandy areas near the high-tide line. Sandy, very saline areas, either entirely open or with scattered *Salicornia* sp. and *D. spicata* also occur at or near this elevation. *Juncus roemerianus* is found scattered as isolated patches throughout the *Sp. alterniflora* zone and as extensive stands at the edge of uplands where regular seepage of fresh water presumably occurs. Above mean spring high tide, *Sp. patens* is dominant. Other species, including *D. spicata*, *Borrichia frutescens* (L.) DC., and *Solidago sempervirens* L. are common in this zone of "high marsh." Scattered shrubs, chiefly *Baccharis halimifolia* L. and *Iva frutescens* L., usually occur in the high marsh, which often gives way to a dense shrub thicket on the adjacent upland.

On tidal creeks away from salt water and on the interior margins of Pamlico Sound, where the tidal amplitude and frequency are irregular and waters are less saline, the pattern of marsh vegetation is different. Here, *Sp. alterniflora* seldom occurs in large stands and is generally confined to the edges of creeks and the area around inlets. In the body of the marsh itself, there are two major vegetation types (Waits 1967). In one, *J. roemerianus* occurs in extensive pure stands just above mean high water. In the other, *Sp. patens* is the dominant, and the vast stands it forms resemble the salt meadows of New England. The substratum typically consists of several inches of brownish peat overlying sand. *Distichlis spicata*, *Sc. robustus*, and *Pluchea purpurascens* (Sw.) DC. are scattered throughout the *Sp. patens* and occasionally may be local dominants. Wet openings, particularly in the Pamlico Sound area, may form favored waterfowl feeding and wintering sites. Along tidal creeks, this basic vegetation pattern is repeated upstream until the limits of regular tidal penetration are reached. There, the salt-marsh species are replaced by those of fresh marshes (*Typha* sp., *C. jamaicense*), and eventually marsh is replaced by Bald Cypress (*Taxodium distichum* (L.) Richard) and gum (*Nyssa* sp.) swamp forest.

4. Florida: The typical marshes of the southeastern Atlantic Coast disappear between Jacksonville and St. Augustine, Florida, where mangroves and several other species are at their northern distribution (Davis

1940, 1943; Egler 1952). Throughout peninsular Florida where mangroves and salt marsh occur together, mangroves exist seaward of the marsh because of their ability to tolerate deeper flooding. Tidal marsh appears to play the role of pioneer in the mangrove zone (Egler 1952), invading after hurricanes and quickly being replaced as a result of shading by mangroves. The northern distribution of mangroves is apparently set by low winter temperatures.

In the vicinity of Cape Canaveral high salt marsh, the habitat of the Dusky Seaside Sparrow (*A. m. nigrescens*), is well developed and extensive (Sykes 1980). The main body of this type of marsh consists of dense *Salicornia* sp., *Batis maritima* L., and *D. spicata*. These species extend inland, intermixing there with *Spartina bakeri* Merr. and *J. roemerianus*. Mangroves, *Avicennia germinans* (L.) L., are widely scattered throughout the marsh. The physical conditions of these marshes are influenced by intermittent flooding by rains and freshwater sheet flow from the uplands and occasional inundations by salt water from adjacent tidal rivers. Heavy doses of salt water occur during storms and as a result of major wind tides. Thus, the habitat fluctuates extensively between flooded and extremely dry and between saline and less saline (Sykes 1980).

In South Florida, salt marshes virtually always occur between a border of mangroves on the seaward side and the vast inland freshwater marshes (Wade et al. 1980). As in North Florida, the habitat fluctuates dramatically from deep and extensive flooding by fresh water or salt water, owing to rains or storms respectively, to extremely dry during the annual rainless season. These marshes are usually dominated by *J. roemerianus*, *D. spicata*, and *Fimbristylis* sp., with *Spartina* sp., *C. jamaicense*, and *Typha* sp. common in the brackish areas (Wade et al. 1980). Frost and fire also influence these marshes. Frost kills back mangroves, thus preventing them from eventually replacing marsh. Fire plays essentially the same role by periodically killing mangroves and favoring marsh species. Coastal prairies, although not true salt marshes (Wade et al. 1980), occur extensively around Flamingo and Cape Sable. In these *Spartina spartinae* (Trin.) Merr. and *Sp. bakeri*, *Borrichia frutescens* and *B. arborescens* (L.) DC., *Sporobolus* sp., and *Batis maritima* are the dominants. These prairies were subject to regular fire in the past and, if protected from fire in the future, are likely to become forests of *Cephalanthus occidentalis* L. (Wade et al. 1980).

The lower west coast of Florida from Tampa south has a mixture of marsh and mangrove on sandy flats or marl over limestone (Davis 1940). North of Tampa the marshes grade into those of the Gulf Coast.

5. Gulf Coast: Salt marshes of the Gulf Coast are basically composed of the same species as occur along the southeastern Atlantic Coast but their proportions are somewhat different. Along the Gulf Coast from Cedar Key to Louisiana, there are extensive stands of *J. roemerianus*. Although *Sp. alterniflora* develops on Gulf Coast beaches where wave action is limited and in extensive areas on the Mississippi coast, most marshes consist of vast stands of *J. roemerianus* grading directly into upland (Kurz and Wagner 1957).

The largest expanses of salt marsh on the Gulf Coast are at the mouth of the Mississippi River (Penfound and Hathaway 1938, Penfound 1952, Shiflet 1963). *Spartina alterniflora* occurs in the areas most regularly flooded by salt water, with vast stands of *Sp. patens*, *D. spicata*, and *J. roemerianus* occupying areas of lower salinity. *Spartina cynosuroides* and *Phragmites communis* Trinius form a zone at the transition to high ground where freshwater seepage occurs. Mangroves occur with *Sp. alterniflora* in areas with high salinity that are protected from wave action.

Marshes similar to those in Louisiana occur in east Texas where rainfall exceeds evaporation. *Spartina spartinae* and *Sporobolus virginicus* (L.) Kunth. are the dominants (Penfound 1952). Although small amounts of marsh occur on the shores of bays and near inlets between Galveston and Corpus Christi, essentially no marsh occurs in extreme southern Texas because of the stress of high temperatures and hypersalinity caused by low rainfall and high evaporation (Hoese 1967).

Role of Salt Marshes in Estuarine Productivity

Considerable research has been conducted on energy flow and nutrient cycling in salt marshes. This research has been extensively published in both the scientific and popular literature and, consequently, the importance of salt marshes in the total estuarine system is reasonably well known. In addition, this research has served as the basis for extensive government management and regulatory programs in the coastal zone.

Studies of salt-marsh function have been carried out along the entire East and Gulf Coasts, particularly at Woods Hole and Sapelo Island and in North Carolina and Louisiana. These show, in general terms, that salt marshes are characterized by high rates of productivity and, at least in the instance of low *Sp. alterniflora* marsh, that the marsh and the adjacent estuarine waters are part of an interrelated system. Salt marshes provide food and shelter both for marsh-inhabiting organisms and for organisms that spend the bulk of their lives in the estuary and adjacent shallow ocean.

Extensive research at Sapelo Island, Georgia, and elsewhere on the East and Gulf Coasts (Cooper 1974) shows the general dimensions of salt-marsh metabolism. Primary production is carried out by marsh grasses and mud-inhabiting algae. In regularly flooded marsh, net primary productivity of the principal species, *Sp. alterniflora*, ranges from 2,000 g/m²/yr in the tall-grass zone along creeks in Georgia (Smalley 1959), to 1,562 g/m²/yr in the tall-grass zone in North Carolina (Stroud 1969), and less than 400 g/m²/yr in entire marshes in Delaware and New Jersey (Morgan 1961, Good 1965). Similar ranges are encountered along the Gulf Coast. Net production of the algae is about 1,600 g/m²/yr in Georgia. Two groups of animals use this net production. Herbivores (grasshoppers and plant hoppers) feed directly on living grass and these, in turn, are eaten by spiders and small birds (sparrows). A small amount (about 5%) of grass productivity moves through this food chain. The vast majority of the energy flow is through the detrital food chain, which begins with the bacterial degradation of *Sp. alterniflora* leaves and stems. These detrital particles and the mud algae are then eaten by detritus feeders such as

fiddler crabs, nematodes, snails, and mussels. These are in turn eaten by larger mud crabs, rails, and Raccoons. A significant portion of detritus is not eaten in the marsh but is washed into the creeks and adjacent estuarine waters by ebbing tides. This exported detritus, plus plankton, feeds the numerous larval and mature fish and shellfish that occur in the estuary, and provides the basis for the contention that salt marshes are a vital component of the estuarine system (Teal 1962). Although the most extensive work on marsh metabolism has been in Georgia, studies elsewhere have generally reinforced this picture and contributed additional detail to our understanding of salt-marsh dynamics.

Recently, however, Nixon (1980) has raised some interesting questions concerning these long-held views of the role of salt marshes in estuarine productivity and water chemistry. Nixon contends that the actual data available to confirm the contention that detritus originating in the marsh is actually exported are at best contradictory. Furthermore, he points out that the concept of the importance of marshes to estuarine productivity was accepted as a fact and implemented in management programs well before conclusive evidence existed. Nixon also points out that there is an apparent contradiction between the generally held view that marshes are net exporters of organic carbon and phosphorus and the view of many that marshes may serve as a sink for these elements and thus can play a role in purifying estuarine waters. After an exhaustive review of the available data, Nixon concludes that salt marshes may well export significant amounts of organic carbon, and that this carbon may well contribute significantly to the standing crop of organic carbon in the water at any one time. However, he argues that such waters do not produce any greater amounts of finfish and shellfish than are produced in coastal areas without major supplements of carbon from salt marshes. Although marsh sediments appear to be sinks for many trace metals, they seem to act as transformers for nitrogen and phosphorus. Nixon's paper makes it clear that, despite our substantial knowledge of salt-marsh metabolism, the picture still has many unclear pieces.

Human Impact on Salt Marshes

Man has modified salt marshes in a variety of ways. Some of these effects, such as harvesting of salt-meadow hay and shellfish, are relatively benign and do not have any long-term negative effect on the marsh ecosystem. Others, however, may be catastrophic in their impact and ultimately may radically alter or even destroy the system.

The most destructive activities in salt marshes are dredging and filling and spoil disposal. These may be associated with navigation projects, with development of commercial or residential land, or with refuse disposal. In all cases there is virtual destruction of the existing marsh as it is smothered with spoil; furthermore, the surface is raised to an elevation at which true salt marsh can no longer survive. Dredging and filling was a major cause of salt-marsh destruction between 1950 and 1970 (Burdick 1967, Chapman 1968, Schmidt 1966). However, in the late 1960s and early 1970s a number of

states (e.g. Massachusetts, New Jersey, North Carolina) enacted laws to regulate dredging and filling. Although not entirely effective, such laws drastically reduced the impact of dredging and filling. They also essentially established a regulatory ban on major modifications of regularly flooded salt marsh on the grounds that those areas are of vital importance to the success of the local fishery industry. These management principles have been carried over and, in some instances, expanded to irregularly flooded marsh, in the coastal-zone management programs approved by the Department of Commerce in the late 1970s.

Mosquito control practices have also had a major impact on East and Gulf Coast marshes. These insects breed in areas of salt marsh at elevations that are intermittently flooded by salt water and in which fresh water from heavy rains can occur. Salt-marsh mosquito control by physical means, therefore, involves either drainage by ditching or flooding by construction of dikes. The purpose of ditching is to dry out the marsh and reduce periods of standing water that induce egg hatching. In regularly flooded marsh such projects can indeed be successful in drying out a marsh (Bourn and Cottam 1950) and causing a shift away from the true marsh plant and animal populations to those characteristic of the irregularly flooded marsh border. The effects of ditching on irregularly flooded marsh are less clear. Although there may be some drying of the system, the ditches increase edge effect and create substantial new artificial creek habitat. Such changes appear to result in increases in production of fish, shellfish, and waterfowl. Unfortunately, spoil placement during such ditching, when done incorrectly, may produce a dike alongside the ditch, impede drainage, and actually contribute to the creation of new mosquito habitat.

Diking of salt marsh for mosquito control may have a different effect (Provost 1968). This practice consists of diking large areas of marsh above the normal high-tide line and impounding fresh or brackish water. Thus marshes of relatively low productivity, which have little interchange with the adjacent estuary, are replaced with highly productive impoundments. Large populations of *Typha* sp. and *Scirpus* sp. invade impoundments with freshwater, and low-marsh species, including *Sp. alterniflora*, may enter brackish impoundments. These are favored habitats for waterfowl and in many cases large populations of desirable fish and shellfish species develop in them.

Research done since 1960 on salt marshes has generally supported, or has been interpreted as supporting, the concept that marshes are an integral part of the total estuarine complex. Such research has provided the technical basis for present programs of estuarine and coastal-zone management. With implementation of these programs the trend toward destruction of salt marshes has been slowed and, in many states, virtually halted. Although coastal-zone management programs alone probably cannot assure the continued protection of East and Gulf Coast salt marshes, there now seems to be a general realization of their value among the public at large. Public support for salt-marsh preservation is our best hope for the perpetuation of sufficient habitat to insure the survival of those populations of Seaside Sparrows that are presently viable.

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The Seaside Sparrow Assemblage: A Review of Its History and Biology

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This symposium is focused on a rather somber-colored, shy and retiring little bird inhabiting coastal salt and brackish marshes from Massachusetts southward to Florida's Cape Sable and thence westward around the Gulf of Mexico to southern Texas. It and the congeneric Sharp-tailed and Le Conte's Sparrows belong to the so-called "grassland group" of Emberizine finches, which also includes the genera *Passerculus* (the Savannah Sparrows) and *Ammodramus* (the Grasshopper, Baird's, and Henslow's Sparrows). The group is fairly well separated from the other finches by morphology and habits as well as by habitat. The Seaside and Sharp-taileds may be regarded as the salt-marsh members of the group, though each is occasionally found in brackish and even freshwater marshes, particularly the Sharp-taileds.

The considerable variation in size and coloration the Seaside species shows throughout its range has given taxonomists no little puzzlement over the years. Currently the complex is divided into nine recognized subspecies, of which only the nominate northernmost race is partially migratory. The others are essentially resident where found, though a few evidence some local movement seasonally. Two races, the Dusky and the Cape Sable, have small, narrow, sharply defined ranges separated from their nearest neighbors by miles of uninhabitable coast; the other seven more or less merge with one another and, though unoccupied stretches of seemingly suitable habitat occur in most of their ranges, they exhibit gradual, poorly marked clines, each with its adjoining neighbor.

The species was discovered and first described by Alexander Wilson, "the father of American ornithology," 170 years ago in 1811 from specimens he collected in the southern New Jersey coastal marshes the year before. His remarks about the bird are still fitting today: "Of this bird I can find no description. It inhabits the low, rush-covered sea islands along our Atlantic Coast, where I first found it; keeping almost continually within the boundaries of tidewater, except when long and violent

east or northeasterly storms, with high tides, compel it to seek the shore. On these occasions it courses along the margin, and among the holes and interstices of the weeds and seawrack, with a rapidity equalled only by the nimblest of our sandpipers, and very much in their manner. At these times also it roosts on the ground, and runs about after dusk."

The first subspecies to be described was discovered near Charleston, South Carolina, a quarter of a century later by the same Reverend John Bachman who also showed Audubon the Bachman's Sparrow and Bachman's and Swainson's Warblers. When Audubon painted and described the form, he named it *macgillivrayi* for the English ornithologist William MacGillivray, for whom he had a high regard (Audubon 1834).

Next came the most strongly marked of the populations, the Dusky, formerly of the area around Titusville, Florida, but now practically extinct thanks to loss of habitat, first through misguided mosquito control measures, and then by wildfires set by the ranchers in the dry season. Although Robert Ridgway of the U.S. National Museum described and named it *nigrescens* in 1873 (Baird and Ridgway 1873), the bird was actually discovered a year earlier by the eccentric (and nonconformist) Massachusetts ornithologist Charles J. Maynard while he was collecting in Salt Lake just northwest of Titusville. He described his experiences with it in an article in "The American Sportsman" in 1875 and named it *melanoleucus*, which though equally fitting, is of course relegated to synonymy.

Fifteen years later in 1888 Joel Asaph Allen of the American Museum of Natural History in New York, the first and longtime editor of *The Auk*, described two of the Gulf Coast races, *peninsulae* from Tarpon Springs, Florida, and *sennetti* from Corpus Christi, Texas. In 1899 Frank M. Chapman, also of the American Museum of Natural History, described *fisheri* from Grand Isle, Louisiana, and in 1919 Arthur H. Howell of the old Bureau of Biological Survey found the most isolated population of the complex at the extreme southern tip of

Florida. He gave *mirabilis* full specific rank, which the A.O.U. Check-list Committee sentimentally maintained in the 1957 *Check-list* as the last "full species" to be discovered in North America. In 1920 Ludlow Griscom and John T. Nichols, both then at the American Museum in New York, named *juncicola* from Wakulla in the Florida panhandle and *howelli* from the Gulf Coast of Alabama. In 1931 Harry C. Oberholser of the Biological Survey described the last valid race, *pelonota*, from New Smyrna Beach, Florida.

Two other names were proposed in 1931, *waynei* from Chatham County (Savannah), Georgia, by Oberholser, and *shannoni* from Duval County (Jacksonville), Florida, by Harold H. Bailey. Both of these have been relegated to synonymy, *waynei* as indistinguishable from *macgillivraii*, and *shannoni* as a brashly fraudulent attempt to invalidate *pelonota*. Bailey printed his papers on his own press in his private museum in Miami. After Oberholser published *pelonota* on October 17th, Bailey printed his account of *shannoni* in his museum bulletin series and dated the issue August 1st. Fortunately Witmer Stone, James Lee Peters, and many other systematists made it a practice to enter the date of receipt on all periodicals as they came in, and nobody received Bailey's publication until December 2nd. For a fuller account of this and some of Bailey's other shenanigans see Hubbard and Banks (1970).

In 1944 Griscom published "A Second Revision of the Seaside Sparrows" based on his considerable experience with the species in the field and a study of what was probably the largest series of specimens gathered together in one place up to that time (and for that matter perhaps to this date). He had 89 specimens from George Lowery's Louisiana State University Collections, plus the extensive series in the Museum of Comparative Zoology, the American Museum of Natural History, and the U.S. National Museum and Fish and Wildlife Service collections. These gave him well over 200 skins that included typical or topotypical material of all the named forms. Recognizing the complexity of the material, he postulated the probable existence of "light" and "dark" forms in most populations. He relegated his own *howelli* and Oberholser's *waynei* to synonymy, but defended retaining *nigrescens* as a full species. His most cogent observation was condemning as "biologically unsound" the recording of aberrant and nontypical individuals in a population as vagrants of other subspecies they seemed to resemble. The 1957 A.O.U. *Check-list* followed his recommendations and assigned *nigrescens* specific rank, and not until 1973 did the Committee see fit to regard all the accepted forms as subspecies of *maritima*. That any further changes will ever be made in its nomenclature seems highly unlikely.

The species' ecology is fairly simple and uncomplicated. The birds live on or near the ground in salt-marsh grasses of the following principal genera: *Spartina*, *Juncus*, *Paspalum*, *Sporobolus*, and *Distichlis*. They are also found in *Batis* (pickleweed) and *Salicornia* (glasswort), in *Typha*, in *Scirpus* rushes, and in low shrub growth of *Baccharis* and *Iva*, particularly when driven out of their preferred habitat temporarily by spring or storm-driven tides. They share this habitat with the Clapper Rail and Long-billed Marsh Wren the year round. Other avian visitors include migrating or winter-

ing Sharp-tailed and Savannah Sparrows, plus black-birds, crows, herons, migrant waders, and occasional foraging hawks and owls.

SPRING. The Seaside's reproductive cycle starts when the days begin to lengthen in mid-February. Northern birds wintering south of their nesting grounds begin their trek back to them, usually arriving by mid-April. South Carolina and Georgia birds leave the outer marshes and move to more protected brackish marshes slightly inland. Most Florida birds are already on territory, the males starting to sing their little buzzing songs from exposed perches, as are the populations around the Gulf Coast.

Courtship and pair formation start when the males begin to sing, in mid-February in the south, a month or two later in the north. Most birds nest in loose colonies, within which males establish both nesting and feeding territories, which they advertise by singing and defend by chasing when necessary. The song, given from a high rush or reed, proclaims the occupancy of the area within which other Seaside Sparrows will not be tolerated. When the warning is disregarded, the male flies directly at the intruder, close to the ground, and uttering rapid chipping notes. The chase is not vigorous and seldom results in bodily contact, for the intruder usually flees.

The defended tract may vary in size depending on its location in the marsh, but is usually about 100 yards in diameter and covers roughly an acre. The region immediately around the nest is the most exclusive, and only one pair of birds occupies it. The feeding territories are in the wet tidal zone and, while both nesting and feeding grounds may be contiguous, birds nesting well back in the marsh often fly 200 yards or more over unsuitable territory to forage. Trost (1968) commented that the individual territory sizes in the Dusky evidently increased as the birds decreased in numbers. Nicholson (MS, 1960s) stated that in the 1930s he often encountered 20 or 25 birds within 100 lineal feet of marsh and found occupied nests within 40 feet of one another.

Trost (1968) banded a number of Dusks on Merritt Island in the early sixties. He found two males banded on territory in 1961 still defending the same territories in 1963. He netted two other males he had banded as juveniles the summer of 1962 defending territories the next year only some 300 yards from where they fledged. He commented: "The main breeding marsh on the Indian River now contains at least four loose colonies of dusks, each isolated one or two miles from the other by stretches of unsuitable habitat. If no interchange of birds occurs, as the banding data suggest, inbreeding must be the rule rather than the exception. And if inbreeding is as prevalent in other seaside sparrows as it seems to be in the dusky, it is easy to see how so many well-marked forms have developed within the species."

NESTING. The literature contains any number of descriptions of the Seaside's nests, most of which are simple open cups of woven grasses built anywhere from a few inches to 1 or 2 feet above the ground, and so well hidden in the thick grass that they are extremely hard to find. Chuck Trost liked to joke that trying to find one was like "hunting for a ball of hay in a needlestack." In the Savannah region Ivan Tomkins (1941) noted that "nests may be built in many different situations . . . from

eight inches above the marsh mud in *Sporobolus-Paspalum* to three feet in *Spartina* or *Juncus* and up to five feet in *Baccharis*." He added that the "top entrance nests are built of the softer grass blades in the vicinity, and when not covered by the natural foliage are canopied. This canopy was more nearly complete where there were heavily incubated sets of eggs, so probably it is added to as incubation progresses. . . . Nests naturally sheltered by the foliage in the tops of *Baccharis* are without canopy." Kopman (1915) described a nest on Battledore Island, Louisiana, "built of grass and the opening, on one side, was rather large. It was four feet from the ground in *Aricinnia nitida*." Nicholson (1946) found nests in mangroves in New Smyrna Beach "from a couple of feet to as high as 14 feet above the mud and water."

EGGS. The clutch varies from two to six eggs, with three or four the most common. Laying dates range from 3 June to 6 July in Rhode Island and Connecticut, 18 May to 19 July in New Jersey, 20 May to 29 June in Georgia, 15 March to 25 July in Florida, and 15 April to 12 July in Louisiana and Texas. This suggests that the northern birds are single brooded, the southern ones multiple brooded.

Nicholson (1946) wrote that at New Smyrna "Nesting usually begins in earnest about the middle of April but sometimes a full set is found by the tenth of April. Nesting continues into August and there is scarcely a day during the nesting period that eggs cannot be found. I have found in different parts of a colony, little areas where most nests held young and in others mostly fresh eggs. This only a few hundred yards apart. Generally speaking the height of the first nesting is April 20th; second sets June 1st, and third sets July 10th to 15th, on into August."

YOUNG. Incubation, by the female alone, may start in some populations before the clutch is complete, but Trost (1968) states that in the Dusky it does not start until the last egg is laid and then normally takes 12 or 13 days. "At hatching the young are pink and show only sparse patches of gray natal down. The egg tooth is shed by the second or third day. On the third day the skin has darkened to almost a bluish gray, but the feather tracts are not obvious until the fourth day. By the sixth day the eyes are open, and on the seventh the feather shafts start to slough off.

"The male helps his mate feed the young, which remain in the nest quietly and are not heard crying for food. They normally remain in the nest about nine days, but by the eighth day are apt to bounce out of it at the least disturbance. Upon leaving the nest they can fly only a few feet, but they scramble actively about in the vegetation and are very difficult to find."

MOLTS. The juvenal plumage in which the young leave the nest is more somber than that of the adults and is clouded with brown streaking. It is replaced in a complete postjuvenal molt that starts in late August. By November the young are indistinguishable from the adults, which have undergone a complete postnuptial molt at about the same time. The duller nuptial dress of spring is acquired entirely by feather wear.

Jonathan Dwight (1900), the pioneer student of molt in the passerine birds, expressed surprise that the Sharp-tailed Sparrow has two complete molts yearly while the

congeneric Seaside Sparrow "living in the same environment . . . and suffering equally from abrasion due to coarse bunch grasses and reeds" has but one. In this connection it is worth noting that all the other grassland sparrows have partial prenuptial molts in which most of the body feathers are replaced, but not the rectrices and remiges. The reason, as Woolfenden (1968) suggested, is that the other sparrows, and particularly the Sharp-taileds, nest and usually forage in the densest stands of grass, while the Seasides do most of their foraging on comparatively open, wet marsh mud where they have less contact with abrasive grasses.

FOOD. The Seasides are outstanding among the Fringillidae for the high proportion of animal food in their diet, which Judd (1901) long ago estimated at over 80%, a figure no student of the birds has questioned since. Audubon (1831) wrote their food "consists of marine insects, small crabs and snails, as well as the green sand beetle, portions of all of which I have found in their stomachs."

Sprunt (1968) wrote: "Small marine life such as various worms, tiny shrimp, and crabs, together with grasshoppers, moths, flies, and spiders compose the bulk of its food. I have watched these birds catch the little moths that flit about the stems and tips of the marsh grass, as well as foraging about on the mud in and out among the stems of grass. Seeds of the cordgrass and glasswort make up part of the vegetable content." Oberholser (1938) said: "The food of this bird reflects the character of its habitat—marine worms, crustaceans, dragonflies, grasshoppers, moths, beetles, bugs, and spiders, with some molluscs." Howell (1928) added crickets, caterpillars, flies, wasps, small crabs, and some weed and grass seeds.

BEHAVIOR. It is hard to improve on Audubon's (1831) general summation: "The monotonous chirpings which one hears in almost every part of our maritime salt marshes, are produced by this bird . . . which may be seen at any hour of the day during the months of May and June, mounted on the tops of the rankest weeds which grow by the margins of the tide waters . . . whence it pours forth with much emphasis the few notes of which its song is composed. When one approaches it, it either seeks refuge amongst the grass, by descending along the stalks and blades of the weeds, or flies off to a short distance, with a continued flirting of its wings, then alights with a rapid descent and runs off with great nimbleness. . . . It is very difficult to shoot them unless when they are on the wing, as their movements while they run up and down the weeds are extremely rapid; but their flight is so direct and level, that a good marksman can easily kill them before they alight amongst the grass again. . . . Having one day shot a number of these birds, merely for the sake of practice, I had them made into a pie, which, however could not be eaten, on account of its fishy savour." This is certainly a revealing commentary on the mores and customs of the day, as well as a confirmation of the birds' diet.

Of its running ability Stone (1937) observes: "While making but little show in the air the Seaside Sparrow is very much at home on the muddy bottom of the marsh, and its large feet are well adapted for running over the

soft ooze while they, as well as the short tail, shape of body, and somewhat elongated bill, all recall the structure of the rails, which are cotenants of the meadows. The Seaside Sparrow can run very swiftly, threading its way in and out among the coarse stalks of the *Spartina* grass that grows along the edges of the creeks. As it runs the legs seem rather long and the body is held well up from the ground while the tail is always pointed downward."

Trost (1968) comments: "During the nonbreeding season the duskies are quite shy, and either remain concealed in the dense vegetation or fly long before one comes near. In the breeding season they become rather tame. Parents with heavily incubated eggs or young in the nest are very bold and will come to within 15 or 20 feet of an intruder at the nest. They perch on the grass tops and nervously twitch their tail and wings, bob up and down, and scold continuously with their metallic *chip-chip, chip-chip* until you leave. For a week or so after the young leave the nest the female will come almost within arm's reach and *chip* incessantly while trying to lead you away.

"After a shower the wet males often sit exposed on the top of the vegetation to fluff and preen their feathers. I watched one such male scratch his head three times, twice over and once under the wing, after which he stretched the same wing out over the extended foot, downward and behind the body."

ENEMIES. The Seaside Sparrow has its normal share of natural enemies. The Common and Fish Crows that forage over the marshes, also the Boat-tailed Grackles and Red-winged Blackbirds, undoubtedly take some eggs and young. The birds of prey that hunt there—American Kestrel, Peregrine Falcon, Short-tailed and Marsh Hawks, Short-eared and other owls—probably get an occasional unwary adult. Raccoons, skunks, and foxes range out into the Seaside habitat when the tide is down and probably account for some nests. Microtine rodents and in the south the Rice Rat also have to be reckoned with. Where the waters have freshened reptiles are encountered—the most frequent snake visitor is the Banded Water Snake, but Ribbon and Garter Snakes, Water Moccasins, and even Pygmy Rattlesnakes have been reported there.

The sparrows have contended with these natural enemies successfully over the ages, but as their numbers dwindle, the effects of predation are magnified. The populations in southern Florida and around the Gulf of Mexico are also affected by the tropical hurricanes that assail their habitat at irregular intervals over the years, but as Stimson (1968) pointed out, while the September 1935 blow extirpated *mirabilis* from its type locality, some birds survived in fresh marshes slightly to the north and westward, where they have managed to weather the worst storms that have struck there in the last half century. The same is true of the Gulf Coast birds, which seem to be able to retreat to the safety of higher ground when the walls of hurricane-driven sea water inundate their homes.

A more serious threat to the Cape Sable is fire, usually man-set, either purposely or accidentally, and exceedingly dangerous in dry years such as the last two (1980 and 1981). The small colony I knew 20 years ago at

Ochopee has evidently been wiped out by successive fires, but recent work by Werner, Bass, Kushlan, and Taylor (this symposium) has shown a thriving population in the center of Everglades National Park, where the birds apparently are dependent on occasional burning to provide the right grassland habitat they need in their freshwater surroundings.

Encroachment by man and his works upon its habitat has been the greatest destroyer of Seaside Sparrows, starting with the filling and draining of the marshes for building that began in the nineteenth century. We have no record of what the Seaside population was like in the great marshes of southern New York and northern New Jersey before industrial growth and pollution made them uninhabitable by any wildlife except possibly non-native rats.

The ditch-draining of the salt marshes for mosquito control that I witnessed in my youth in Massachusetts started a cycle of drying the marshes that shrunk the Seaside's preferred habitat steadily, especially near cities, towns, and shore resorts. The diking of the Merritt Island marshes to eliminate the Salt-marsh Mosquitoes by impounding fresh water on the marsh had even more unfortunate results. Started in the 1920s to create agricultural land, the dikes were not completed until the late 1950s, but they signaled the start of the Dusky's decline, which reached its denouement in the last decade, as Sykes (1980) so ably delineated. Large Pig Frogs moved into the fresh impoundments, and the dikes were soon covered with brush growth in which Boat-tailed Grackles and Red-winged Blackbirds started nesting close to the Dusky colonies.

The end of World War II released DDT in quantity for public use as an insecticide, and its effects were soon apparent on much more than the mosquitoes it was broadcast to control (see Rachel Carson's *Silent Spring*, 1962). Nicholson (1950) was the first to note the decline of the New Smyrna Seasides. "As recent a date as 1939, hundreds of birds still bred in this marsh, but since that date have become increasingly fewer in numbers, and during the springs of 1948 and 1949, when repeated searches were made by both Wray H. Nicholson and myself, not a single bird, nor even an old nest was in evidence. They have completely disappeared."

From the mid-1940s through the 1950s the marshes along the Indian and Halifax Rivers were repeatedly and heavily sprayed with DDT from Merritt Island northward to Daytona and Ormond Beach. Chuck Trost and I searched these marshes persistently from 1959 well into the 1960s, and failed to find a single breeding pair between Matanzas Inlet and the few surviving Dusks on Merritt Island. In the late 1960s and early 1970s I found scattered remnants of the *pelonota* population breeding in small colonies in the few suitable marshes remaining from Matanzas Inlet northward some 70 miles to the Georgia-Florida boundary. Recent Audubon Christmas Bird Counts show the species apparently still doing fairly well in the marshes northeast of Jacksonville, where from 10 to 50 birds are reported annually. In 1975 and 1976 Kale (this Symposium) surveyed the marshes from New Smyrna northward and found no breeding Seasides south of the St. Johns River in Duval County, but north of the St. Johns the birds were plentiful.

Few modern bird-watchers relish slogging into the Seaside habitat, and the marshes have not been adequately censused in recent years. The birds are on the Florida "Species of Special Concern" list because of the fragility of their habitat. Human pressure on that fragile environment is continuing to increase, and the Seasides should certainly be placed with the other grassland sparrows on the "Blue List" of threatened species to alert those most concerned about the situation so that the necessary drastic steps may be taken before the rest of the complex joins the Dusky in oblivion.

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Distributional Evolution of the Seaside Sparrow

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Abstract: The suggested course of subspeciation in the Seaside Sparrow (*Ammospiza maritima*) is as follows: (1) The species diverged from polyphasic Savannah Sparrow stock in the late Pliocene or early Pleistocene and spread until it occupied the Atlantic and Gulf Coasts from North Carolina to Louisiana. (2) The complete emergence of the Florida peninsula split the ancestral polyphasic population into Atlantic Coast and Gulf Coast populations, each having birds with light, intermediate, and dark color phases. (3) Stabilization of the various habitats and resulting selection operated in some situations to favor either the dark or the light phase. (4) The polyphasic Atlantic Coast stock, now considered to be *A. m. macgillivraii*, gave rise to the dark races *A. m. pelonota* and *A. m. nigrescens* as well as to the pale race *A. m. maritima* and the birds attributed to the invalidated "waynei" race. (5) The polyphasic Gulf Coast stock (*A. m. fisheri*) gave rise to the dark races *A. m. peninsulae* and *A. m. juncicola* and to the pale races *A. m. mirabilis* and *A. m. sennetti*. This hypothesis concurs with current taxonomy, which treats the Seaside Sparrow populations as one species, and offers a logical explanation for the distributional pattern of the various color phases.

Seaside Sparrows of the genus *Ammospiza* have been the subject of considerable taxonomic study. Chapman (1899) published the first report on the genus as a whole. He recognized three species, *Ammospiza nigrescens*, *A. sennetti*, and *A. maritima*. *Ammospiza maritima* was further subdivided into four subspecies. Griscom and Nichols (1920) published a revision of this group and again recognized three species, but *sennetti* was reduced to subspecific status under *maritima*. They recognized *A. nigrescens*, *A. mirabilis*, and *A. maritima* as full species and listed seven subspecies of *maritima*, two of which were described as new (*A. m. juncicola* and *howelli*). Oberholser (1931) discussed the status of the Atlantic Coast races of *maritima* and described two new subspecies, *A. m. waynei* and *A. m. pelonota*. In a second revision of the entire group of Seaside Sparrows, Griscom (1944) recognized *howelli* as the light phase of *A. m. fisheri* and established Oberholser's *waynei* as the light phase of *A. m. macgillivraii*. The Fifth Edition of the *Check-list of North American Birds* (A.O.U. 1957) accepted most of the findings of Griscom (1944) and listed three species, *A. mirabilis*, *A. nigrescens*, and *A. maritima*, with *maritima* divided into seven subspecies. This taxonomy was not changed until the appearance of the Thirty-second Supplement to the 1957 *Check-list*

(A.O.U. 1973). *Ammospiza nigrescens* and *A. mirabilis* are now considered subspecies of *A. maritima*; the Seaside Sparrow group thus becomes one species with nine recognized subspecies. We concur in this decision and offer in this paper substantiating reasons for our concurrence. The names and ranges used for discussion purposes will be those of the 1957 *Check-list* and its 32nd Supplement (Table 1), although this analysis of the distributional evolution of the Seaside Sparrow was made more than a decade prior to publication of the 1973 supplement.

COLOR PHASES

Seaside Sparrows display a wide and confusing range of color variations both between and within the races. Three major color phases are recognized by taxonomists—light, dark, and intermediate. Color characters are far more useful in working with these birds than linear measurements or proportions, but all of these characters in combination with the breeding ranges, have been used in distinguishing the various races (Table 2). Previous attempts to establish a regular geographic progression of races and to suggest their phylogenetic relationships have been limited and unsa-

TABLE 1. Breeding-season distribution of Seaside Sparrow subspecies.

Northern Seaside Sparrow, <i>Ammospiza maritima maritima</i> (Wilson 1811)*	Massachusetts to Virginia
MacGillivray's Seaside Sparrow, <i>A. m. macgillivrayi</i> (Audubon 1834)	Dare County, N.C., to southern Georgia
Smyrna Seaside Sparrow, <i>A. m. pelonota</i> (Oberholser 1931)	Northeastern Florida, Amelia Island to New Smyrna
Dusky Seaside Sparrow, <i>A. m. nigrescens</i> (Baird and Ridgway 1873)	Formerly in central eastern Florida, eastern Orange and northern Brevard Counties
Cape Sable Sparrow, <i>A. m. mirabilis</i> (Howell 1919)	Southern tip of Florida, especially in certain freshwater marshes of the Everglades region
Scott's Seaside Sparrow, <i>A. m. peninsulae</i> (Allen 1888)	Gulf Coast of Florida, Pepperfish Key to Old Tampa Bay
Wakulla Seaside Sparrow, <i>A. m. juncicola</i> (Griscom and Nichols 1920)	Gulf Coast of Florida, Escambia Bay to southern Taylor County
Louisiana Seaside Sparrow, <i>A. m. fisheri</i> (Chapman 1899)	Pensacola, Florida to San Antonio Bay, Texas
Texas Seaside Sparrow, <i>A. m. sennetti</i> (Allen 1888)	Nueces and Copano Bays, Texas

*For references to authorities for subspecies, see McDonald's bibliography elsewhere in this publication.

tisfactory (Griscom and Nichols 1920, Tomkins 1937 and 1941, Griscom 1944, Beecher 1955).

We have been engaged in field studies of MacGillivray's Seaside Sparrows (*A. m. macgillivrayi*) on the North and South Carolina coasts for a number of years (Quay 1953, Funderburg and Quay 1959, Funderburg 1981). We have attempted to understand the distribution of populations of *macgillivrayi*, and to ascertain the relationships of these sparrows to the adjacent races on the Atlantic Coast. These studies have led us to believe that the mode and sequence of subspeciation in the Seaside Sparrow have not been properly explained.

The *Emberizinae* is a very plastic group. The Song Sparrows (*Melospiza melodia*) and Savannah Sparrows (*Passerculus sandwichensis*), in particular, are noted for their differentiation into many races showing a great range of color variation (Aldrich 1940, Johnston 1956a and 1956b, Norris and Hight 1957, Marshall 1948a and 1948b, Van Rossem 1947). It seems probable that the ancestral Seaside Sparrow evolved in the eastern United States as a salt-marsh derivative of the Savannah Sparrow. Modern research has conclusively proved that there is a complete chain of intergrading characters between the western races of the Savannah Sparrow on the mainland and the salt-marsh variants of this species in Baja California (Beecher 1955, Peters and Griscom 1938, Van Rossem 1947). The initial isolation of the ancestral Seaside Sparrow from the Savannah Sparrow has been suggested to have occurred during the late Pliocene and early Pleistocene (Howard 1947, Martin 1958). The ancestral sparrow may have been a heterogeneous bird in regard to color phases, and it has been recognized that the ancestral bird probably had at least two color phases (Griscom 1944). However, it is also possible that the ancestral Seaside Sparrow could have been either dark or light. A single mutation could have produced an intermediate form (the heterozygote), which would then generate all three color types in subsequent generations.

GEOLOGIC HISTORY

Knowledge of the Pleistocene geology of the southeastern coastal plain has advanced considerably since Cooke (1945), Goin (1958), and Neill (1957) published their thoughts on the submergence of much of peninsular Florida and its effects on present-day biogeography. Nevertheless, the basic premise that central Florida was isolated from the mainland seems indisputable, and whether this was from the insular pattern proposed by these authors or simply by ecological isolation resulting from low lands through the Suwannee Basin makes little difference in interpreting overall present-day faunal distributions.

Florida probably has persisted as a peninsula or major island since Hawthorne times (middle Miocene). As numerous authors have noted, Pleistocene sea levels fluctuated throughout the ice ages. This undoubtedly had a tremendous impact on salt-marsh systems. It allowed them to vary from extensive marshes spreading out when large areas of the Florida Plateau were exposed to ones perhaps more reduced than those we see today. Nevertheless, contrary to earlier beliefs, maximum sea levels probably never rose more than 10 feet above the present levels during the entire Pleistocene (R. Franz and D. Lee, pers. comm.; see Alt 1968).

Through a low, marshy corridor of what is now the Okefenokee Swamp and the Suwannee and St. Marys River Basins, Seaside Sparrows and other marsh inhabitants apparently had the opportunity for a continuous genetic exchange between Gulf and Atlantic Slope populations during periods of high seas. Swamping of the northern Florida peninsula occurred off and on from the Miocene through the early Pleistocene. Thus we propose that the present-day similarity between *A. m. fisheri* on the Gulf Coast and *A. m. macgillivrayi* on the Atlantic Coast is the result of regular genetic exchange through at least the early Pleistocene, which allowed the three color phases to remain viable throughout this "population." It is possible that the ancestral stock was, in fact,



Fig. 1. Distribution of the races of the Seaside Sparrow.

TABLE 2. Distinguishing characteristics of Seaside Sparrow subspecies.

Name	Underparts			Dorsum	Color phases
	Basic color	Buff wash	Streaking		
<i>A. m. maritima</i>	Grayish white	Suffused with light buff	Grayish, indistinct	Grayish olive shaded with fuscous, without distinct black streaks	Light
<i>A. m. macgillivraii</i>	Grayish white	Suffused with light buff	Grayish olive, distinct	Pale olive gray without streaking	Light
	Dark	Suffused with light buff	Grayish olive, distinct	Dark olive gray, heavily streaked with black	Intermediate
<i>A. m. pelonota</i>	Grayish white	Faint tinge	Grayish, distinct	Grayish brown, heavily streaked with black	Dark
<i>A. m. nigrescens</i>	White	None	Black, heavy, sharply defined	Black or brownish black; no yellow around eye	Dark
<i>A. m. mirabilis</i>	White	None	Black, narrow, sharply defined	Yellowish olive streaked with fuscous; distinct yellow area around eye	Light
<i>A. m. peninsulae</i>	White	Suffused with brownish ash	Black, narrow, sharply defined	Dark olive overlaid with dark cinnamon brown	Dark
<i>A. m. juncicola</i>	Gray	Faint tinge	Black, diffuse	Fuscous black; dark olive on nape and rump	Dark
	Dark	Pale, dull, buff	Black, heavy	Dark brown, broadly streaked with fuscous black	Dark
<i>A. m. fisheri</i>	Gray	Bright ochraceous	Black, diffuse to unstreaked	Head and nape cinnamon brown, back mummy brown	Intermediate
<i>A. m. sennetti</i>	Grayish white	Most—none; few—faint yellowish buff	Chest—none; sides—distinct, narrow, black	Greenish gray, nape distinctly streaked with black	Light

this one continuous population. The other races of Seaside Sparrows diverged, colonizing extensively developed marshes of the Gulf Coast and peninsular Florida during low sea levels. Rising sea levels restricted marsh systems, leaving isolated populations to develop distinct genetic identities. The most recent major rise in sea level was in the last 10,000 years, so it is possible that current isolation and genetic divergence only recently stabilized. The arrival of the Red Mangrove (*Rhizophora mangle*) in tropical Florida, apparently a rather recent occurrence, provided additional ecological isolation for sedentary, marsh-dependent sparrow populations in the southern portion of Florida. The spread of this tree also greatly restricted the amount of coastal habitat available.

We propose, therefore, that the evolutionary development of *Ammospiza maritima* is a result of both geological and ecological factors. The changing shoreline of the southeastern coastal plain provided broad corridors for dispersal and colonization during glacial (low) seas, and also restricted habitats—or at least fragmented them—during interglacial (high) seas. The exception to this was the nearly continuous marsh system across northern Florida during high seas, which allowed genetic exchange between faunal populations in the regions now occupied by *A. m. fisheri* and *A. m. macgillivraii*. Thus these populations maintained their genetic similarity to the parental stock while, simultaneously, elsewhere along the Gulf and Atlantic Coasts other populations were being isolated. Ecological differences in habitats favored certain color phases, and ecological extremes fragmented and isolated populations.

EVOLUTION OF RACES

It seems probable that the polyphasic Atlantic Coast group gave rise to the ecologic races along the Atlantic Coast, and the polyphasic Gulf Coast group to those along the Gulf Coast. Both coasts still have a polyphasic race, and these two nominal populations—*A. m. macgillivraii* on the Atlantic Coast and *A. m. fisheri* on the Gulf Coast—resemble each other in producing numerous individuals that must be classed as “intermediate.” None of the other races has three color phases. Each of these polyphasic populations also occupies the largest geographical range on its respective coast, *macgillivraii* ranging from northern North Carolina at least to southern Georgia and *fisheri* from Pensacola, Florida, at least to the vicinity of Galveston, Texas. In addition, the two races strikingly resemble each other. Numerous Gulf Coast birds have been incorrectly identified as *macgillivraii*, and a number of South Carolina specimens as *fisheri* (Griscom and Nichols 1920).

The difficulty of separating these two races was pointed out by Wayne (1910) in his discussion of supposed *fisheri* from South Carolina: “This supposed race very closely resembles *P. m. macgillivraii* from which it differs in having the chest, sides, and flanks buffy or ochraceous. Audubon found it in Texas and Louisiana and referred it to *macgillivraii*. I have taken near Mount Pleasant numerous typical specimens in the autumn and spring months. A ‘typical’ specimen was taken on October 27, 1893, and another on April 16, 1901, thus indicating the southward, as well as the northward migration. It is my belief that *fisheri* is a

synonym of *macgillivraii* Audubon, as it occurs in South Carolina in company with *macgillivraii* and must breed to the northward of this state, perhaps in southern North Carolina. If the birds I have taken on this coast are not migrants from Louisiana and the Gulf coast of Florida, then they must breed somewhere on the Atlantic coast.”

After the emergence of the Florida peninsula separated the ancestral polyphasic stocks, they probably spread rapidly, as the various shorelines became stabilized, until large parts of the Atlantic and Gulf Coasts were occupied. The environments were not uniform throughout the ranges of these two groups, however, and as the marshes became stabilized those color phases best suited to a particular environment became dominant, whereas the other color phases were greatly reduced if they did not die out altogether. The polyphasic stocks evidently occupied the least extreme environments where no selection toward a particular color phase occurred.

Another break of great significance occurred, however, when the range of the Atlantic Coast population was again split into two polyphasic segments. The shoreline of South Carolina from the northern border of the state to Georgetown, an airline distance of about 100 miles, became uninhabitable to Seaside Sparrows, as it is today. The ocean beats directly on the mainland, and the few salt marshes are poorly developed, limited in extent, and unable to support any Seaside Sparrows (Dingle and Sprunt 1932, Sprunt and Chamberlain 1949, Tomkins 1937, Wayne 1910).

Beecher (1955) discusses the late Pleistocene factors such as drowned rivers and coastal upwarplings, which may have been the initial causes of splitting some of the parental stocks into various geographical races. Tomkins (1934) evaluates the effects of hurricanes as another possible factor initiating subspeciation in this group. There are some breaks between races, however, that do not seem to be a result of any of these factors. It is well known that Seaside Sparrows are found only within a very narrow range of habitat conditions (Tomkins 1941, Woolfenden 1956). We are of the opinion that detailed ecological study of the seemingly suitable habitat separating two subspecies, such as *A. m. juncicola* and *A. m. peninsulae*, would reveal that the absence of one or more essential habitat requirements renders the intervening marshes unsuitable for Seaside Sparrows.

Subspeciation in this group has probably occurred as a result of spatial isolation resulting from habitat barriers, rather than from geographic barriers (Mayr 1947). Whether genetic isolation has also occurred is not known. However, many of these races are so poorly differentiated from each other that it seems doubtful that full genetic isolation has been attained. Any or all of these races would probably interbreed if their ranges came into contact (see Webber and Post, this symposium).

The North Carolina segment of the *A. m. macgillivraii* population still contains light, intermediate, and dark birds all breeding together (Tomkins 1937, Griscom 1944), and it is probably from this segment that *A. m. maritima* has evolved as a pale race derived from the light phase of migratory *macgillivraii*. It is possible, of course, that *maritima* was derived directly from

the polyphasic ancestral stock; but several facts lend credence to the idea that it was derived as a northward extension of *macgillivraii*: (1) *maritima* is the only Atlantic Coast race breeding north of the Carolinas, (2) it is the only race that winters largely outside its breeding range, and (3) its winter range lies mostly within the range of *macgillivraii*.

The listed extension of the breeding range of *maritima* southward into North Carolina in the 1957 Checklist is not supported by the literature and is not justified for two reasons. (1) Elizabeth City is too far inland for breeding Seaside Sparrows, especially in regard to the lack of salt-marsh community indicator species in the area. (2) There are no records of Seaside Sparrows breeding in North Carolina outside the coastal salt marshes. In addition, Duvall (1937) made a search from Pungo, Virginia, to Oregon Inlet, North Carolina, and found no Seaside Sparrows until he reached Oregon Inlet. In 1976 and 1977, David S. Lee (pers. comm.) conducted a similar survey, including the Elizabeth City locality, and was unable to find Seaside populations. A Breeding-bird Foray sponsored by Carolina Bird Club in June 1980 also recorded no Seaside Sparrows in the Elizabeth City-Currituck Sound area (Eloise Potter, pers. comm.).

The South Carolina-Florida polyphasic population has given rise to various populations. Seaside Sparrows of the South Carolina and Georgia coasts are all pale olive birds closely resembling *maritima* and were given subspecific status by Oberholser (1931). Griscom (1944) invalidated Oberholser's *waynei* on the basis that it was only the light phase of *macgillivraii*. That this population is derived from the light phase of polyphasic *macgillivraii* seems likely, and on this basis "*waynei*" and *maritima* resemble each other only because both forms probably evolved from the same color phase of *macgillivraii*. The important factor is that they have evidently evolved independently of each other.

Ammospiza m. pelonota and *A. m. nigrescens* are both dark birds probably derived from the dark phase of the polyphasic ancestor. Both races represent small, local populations. The first lives on muddy islands covered with *Salicornia* and *Batis maritima*, with a scattering of stunted mangroves, a totally different environment from the *Spartina alterniflora* marshes of South Carolina and Georgia. Its chief character is its smaller size. The second is an extreme development of the dark phase, having heavy black streaking on a white breast and lacking the yellow postocular stripe. Prior to its apparent extirpation (see Kale, this symposium), *nigrescens* was restricted to the marshes in the vicinity of Merritt Island and the Saint Johns National Wildlife Refuge in Florida.

Several races have also evolved on the Gulf Coast, of which *A. m. fisheri* alone is still polyphasic. The dark, intermediate, and light phases of *fisheri* breed together only in the central and eastern parts of the range of this group. At the western limits of its range, only the pale phase has been found (Griscom 1944). Therefore, *A. m. sennetti*, a pale bird on the southern coast of Texas, seems to have evolved from the light phase of *fisheri*. Strong support for this hypothesis is given by Griscom (1948). In his study of a large series of *sennetti*, he discovered that birds of this race from San

Antonio Bay northward intergrade with light-phase *fisheri*.

Ammospiza m. peninsulae on the west coast of the Florida and *A. m. juncicola* on the Gulf Coast of the Florida panhandle are both dark subspecies seemingly derived from the dark phase of the polyphasic Gulf Coast ancestral stock. Both races inhabit dense stands of *Juncus roemerianus*, which Griscom (1944) has called "the densest marsh vegetation in North America."

Palest of all the Seaside Sparrows is *A. m. mirabilis*. Griscom (1944) states: "While it is the greenest of seaside sparrows, duller specimens cannot be distinguished above from the most olive *sennetti*." It seems evident that *mirabilis* on the Gulf Coast is also derived from the light phase of the polyphasic stock; thus, its resemblance to *sennetti* in some respects is not surprising.

One of the most difficult obstacles in setting up a regular geographic progression of races for this group has been the *A. m. nigrescens*-*A. m. mirabilis* complex in Florida. On the east coast is *nigrescens*, the darkest of all the Seaside Sparrows; on the southwestern coast is *mirabilis*, the palest. These two populations, both at the limit of breeding range for the species on their respective coasts, are very small in numbers. The small population size and strong geographic isolation probably have been conducive to rapid rates of evolutionary divergence. In view of this strong geographic isolation and these subspecies' sedentary nature, it does not seem likely that either race gave rise to the other. According to our hypothesis, *A. m. nigrescens* represents the southern extreme of the Atlantic Coast populations, and *A. m. mirabilis* the eastern extreme of the Gulf Coast populations (Fig. 1 and 2).

There probably are two ways in which these ecologic races have developed from the ancestral polyphasic sparrow: (1) The populations could have been spatially isolated in a suitable habitat very early in the history of the group. If, as the habitat developed, there was strong selection against certain color phases, then those color phases eventually would have disappeared, resulting in a homogeneous population. This may have been the case with *A. m. nigrescens* and *A. m. mirabilis*, in particular, because these two races have diverged far enough from the ancestral stock to have been considered taxonomically as full species until 1973. (2) The polyphasic stock could have spread gradually from its original site of isolation as the habitat developed, and under different environmental gradients strong selection against particular color phases could have occurred, resulting in one or more uniform populations. This may have been the case with races such as *A. m. maritima* and the "*waynei*" population, both pale olive birds that resemble each other closely but have seemingly evolved independently of each other from the light phase of polyphasic *macgillivraii* stock. In either case, the end result would be the same.

The few attempts to explain the inheritance of the various color patterns are descriptive in nature and very general (Griscom and Nichols 1920, Tomkins 1937). In the absence of controlled breeding experiments, it is possible only to infer the genetic basis of color inheritance. The fact that there are three color phases (light, intermediate, and dark) and the intermediate form has

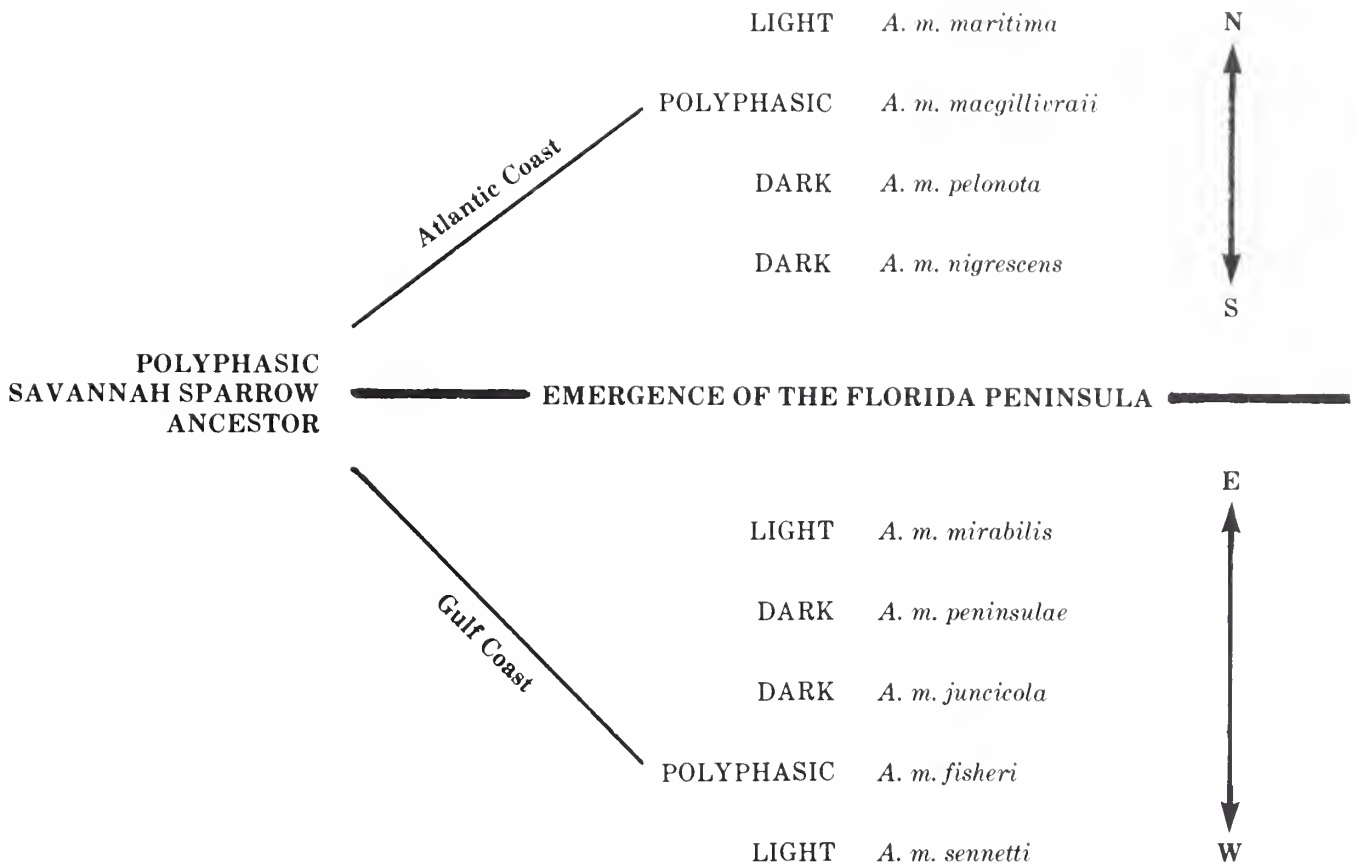


Fig. 2. Phylogeny of the Seaside Sparrow (*Ammodramos maritima*).

never been found as a pure colony suggests that only one gene pair is involved in the inheritance of these phases. Griscom (1948), reporting on a collection of 65 polyphasic *fisheri* from Matagorda, Texas, discusses these birds in relation to their closeness of fit into light, intermediate, and dark categories. He does not discuss the arrangement of these birds from a genetic viewpoint and admits that some of his decisions were arbitrary. Nonetheless, in general, the birds in this particular collection very closely approach a 1:2:1 genetic ratio—one light (19 birds): two intermediate (32 birds): one dark (14 birds). Van Rossem (1947), in his discussion of the salt-marsh Savannah Sparrow (*P. s. sanctorum*), a dichromatic race, notes that there was a ratio of approximately three pale gray birds to one brown in 80 specimens of this race.

Because there is in the Seaside Sparrow a gradation between dark and intermediate and between intermediate and light, it is also possible that these characters depend on the action and interaction of multiple genes, which may vary in expression from individual to individual as well as from race to race. Typically, these genes are subject to considerable phenotypic modification by environment (Srb and Owen 1957).

ZOOGEOGRAPHIC PARALLELS

Several other vertebrate species exhibit a distributional pattern similar to that of the Seaside Sparrow. Although none exactly mirrors the current distribution

of *A. maritima*, collectively they suggest similar biogeographic histories. From the north, several interior species reach the southern limits of their range largely in salt marshes along the Atlantic Coast. Marsh Hawks (*Circus cyaneus*), Tree Swallows (*Iridoprocne bicolor*), Sharp-tailed Sparrows (*Ammodramos caudacuta*), and Swamp Sparrows (*Melospiza georgiana*) all extend their ranges southward in salt-marsh habitats or tidewater communities to the Delmarva Peninsula. The Meadow Vole (*Microtus pennsylvanicus*) avoids the coastal plain south of the Dismal Swamp area but is found along the Outer Banks of North Carolina and has relict populations at Charleston, South Carolina, and on Cedar Key, Florida (Woods et al. 1982). Although most of these populations show no evolutionary differentiation (except in the Swamp Sparrow and in the Florida population of the Meadow Vole), they do illustrate that coastal marshes provide suitable habitats in areas that are otherwise south of the species' normal range. We propose that the ancestral stock of the Seaside Sparrow had a similar expansion into this coastal fringe community from an interior stock.

Other species illustrate similar evolutionary histories in that they have fragmented coastal populations. Several of the species in this group are also representatives of northern stocks that extended their natural ranges southward along the coastal marshes. The Long-billed Marsh Wren (*Cistothorus palustris*) is interesting in that it has an inland race (*C. p. iliacus*) and five

named coastal races that extend from New England to the Chesapeake Bay (*C. p. palustris*), the North Carolina coast (*C. p. waynei*), the southern Atlantic from South Carolina to north Florida (*C. p. griseus*), and the Gulf Coast, where there are two races (*C. p. marianae* and *C. p. thryophilus*). The Clapper Rail (*Rallus longirostris*), which has five coastal races, ranges like the Seaside Sparrow from New England to Texas. The Diamondback Terrapin (*Malaclemys terrapin*) has seven races. The breaking points between the named populations of these species closely parallel those of the Seaside Sparrow. Turtles of the River Cooter complex (*Chrysemys concinna*) should also be mentioned. Although they range far inland along coastal streams, they do exhibit interesting zoogeographic distributional patterns that could easily be explained by changing shorelines and the effect of the isolation of peninsular Florida. The isolation of peninsular Florida also apparently led to the development and fragmentation of the "Salt Marsh Water Snake" complex, races of *Nerodia fasciata* of Florida and the Gulf Coast. Perhaps most intriguing is the Marsh Killifish complex (*Fundulus confluentus/pulvereus*). *Fundulus confluentus* occurs throughout coastal and interior peninsular Florida whereas *F. pulvereus* is confined to the coastal fringe from the lower Chesapeake Bay to the central Texas coast, excluding Florida. In the western panhandle of Florida, however, it intergrades with *F. confluentus*. Thus, as apparently occurred in the ancestral Seaside Sparrow, identical populations occupy the Atlantic and Gulf Coasts, with an intervening stock occupying peninsular Florida. Relyea (1965) presented evidence that these two *Fundulus* are conspecific, although the populations are recognizable. Similar distributional patterns are available in the *F. grandis/heteroclitus* species pair. For distributional maps and further information, see Lee et al. 1980.

CONCLUSIONS

It is not our intent to reduce the complex coastal zoogeographic history to the simple model we present for the Seaside Sparrow. We merely want to point out that this sparrow is only one of several members of the East Coast fauna that exhibit a complex distributional and evolutionary history. Because of the current distributional and evolutionary spectrum of these species, we assume that the situation is not static.

The genetic explanation of the inheritance of color phases in the Seaside Sparrow must remain highly speculative until several kinds of research have been completed. These include intensive studies of marked birds on their breeding grounds, selective collecting of breeding birds, and crossbreeding experiments in the laboratory. Several papers on the agenda of this symposium show that the research effort is well under way.

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PART II

Biology of the Seaside Sparrow

Distribution and Migration of Seaside Sparrows

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Abstract. The majority of the nine presently recognized races of the Seaside Sparrow (*Ammodramus maritima*) are so similar to neighboring races that individual birds outside their known breeding range cannot be subspecifically identified with certainty. The northern race, *A. m. maritima*, is partially migratory, with most individuals departing in autumn from Chesapeake Bay and from all the coastal marshes that lie to the north of the mouth of this bay. No banded bird has been recaptured in winter south of its breeding locality, however, so even the major wintering ground of this subspecies cannot be defined. The other subspecies are presumed to be primarily sedentary.

Median arrival and departure dates at Fairfield, Connecticut, are 18 May and 19 September. On Long Island, New York, the spring peak occurs in the third week of May, and the autumn peak in mid-October. Postbreeding wanderers of unknown origin move north and east in August and September to the coastal marshes of Maine, New Brunswick, and Nova Scotia. The remarkably few records away from tidewater are from North Carolina, eastern Pennsylvania, the lower Hudson River, and eastern Massachusetts.

In the 170 years that the Seaside Sparrow (*Ammodramus maritima*) has been known to science, it has had an exciting history. Each of the five editions of the A.O.U. *Check-list* has recognized a different set of subspecies. Descriptions of geographic ranges have shifted back and forth as new populations were discovered and as habitat loss drove breeding populations from their former haunts. Major changes in the classification and known breeding distribution, as summarized in the various editions of the *Check-list*, are reviewed here, with the help of a series of maps (Fig. 1). The fact that some populations of the Seaside Sparrow are migratory was not recognized until the Third Edition of the A.O.U. *Check-list* (1910), and even now the wintering areas of the various subspecies are very poorly known.

HISTORY

Breeding Range

Alexander Wilson first described the Seaside Sparrow, which he called *Fringilla maritima*, in 1811. The type locality, "sea islands along our Atlantic coast," has been interpreted to mean New Jersey. Twenty-three years later Audubon (1834) described the south Atlantic Coast race *macgillivraii* as a distinct species *Fringilla Macgillivraii* from the salt marshes of the Carolinas,

with the type locality believed to be Charleston, South Carolina.

Nearly 40 more years passed before the discovery of the Dusky Seaside Sparrow, which Baird and Ridgway (1873) called *Ammodramus maritimus* variety *nigrescens*, rather than a distinct species. The type locality was Indian River, Florida.

The First Edition of the A.O.U. *Check-list*, published in 1886, did not recognize subspecies, but did recognize *nigrescens* as a distinct species on the basis of a second paper by Ridgway (1880). The range of *nigrescens* was given as "Salt Lake, Southern Florida." The range of the other species, *Ammodramus maritimus*, was given as "Salt marshes of the Atlantic coast, from Massachusetts southward, and along the Gulf coast to the Rio Grande."

Dr. J. A. Allen (1888) described two additional subspecies of the Seaside Sparrow. The first, *peninsulae*, was based on two females collected at Tarpon Springs just northwest of Tampa Bay on 28 February 1888 by W. E. D. Scott. Allen described these as intermediate between *maritimus* and *nigrescens* but approaching the latter more nearly than the former. Furthermore, he suggested that material from other points might eventually bridge the gap between these two forms and that *nigrescens* would prove to be merely a subspecies of

maritimus as originally described by Ridgway. Allen also found in George B. Sennett's collection a specimen collected "many years since" at Cedar Keys in November that is practically identical to the Tarpon Springs birds.

It is interesting that after the above account was set in type Allen received from Dr. A. K. Fisher 16 Seaside Sparrows collected at Grand Isle, Louisiana, 6 to 9 June 1886. Allen considered these to be the same subspecies as the Tarpon Springs birds. Allen lamented that his name *peninsulæ* was not happily chosen because this form was not restricted to the Florida peninsula but occurred westward at least to western Louisiana.

On the basis of a single pair of birds taken at Corpus Christi, Texas, on 25 May 1882, and a juvenile taken there on 14 June 1887, all by George B. Sennett, Allen described the new race *sennetti* from the "Gulf coast of Texas (Corpus Christi)."

Authors of the Second Edition of the A.O.U. *Check-list* (1895) basically followed Allen, but chose to ignore Audubon's race *macgillivraii* and in so doing made the mistake of overlapping the breeding ranges of *maritimus* and what they considered to be the Atlantic population of *peninsulæ* (Fig. 1). *Maritimus* was described as occurring south to the coast of Georgia, and *peninsulæ* was assigned a range from South Carolina to northern Florida as well as on the Gulf Coast from Florida to Texas.

Frank M. Chapman (1899) tackled a revision of the Seaside Sparrow based on 160 specimens and on his field experience with four of the five recognized forms. He recognized three distinct species: *nigrescens*, *sennetti*, and *maritimus*. He found *sennetti* to be abundant and breeding in the marshes of Nueces Bay, Texas. Finding no evidence whatever of its intergradation with any of its congeners, Chapman had no reason for denying it specific rank.

Chapman pointed out that *maritimus* nests regularly in Rhode Island and as far east as Westport, Massachusetts, and he clarified that the Georgia locality given in the Second Edition of the *Check-list* was based on nests and eggs taken at St. Mary's, Georgia, by William Brewster. Ridgway had extended the southern limit to northern Florida, apparently based on Lt. Robinson's breeding specimens from St. Augustine and Matanzas Inlet.

Chapman cleared up some of the confusion over the race *peninsulæ* by pointing out that none of the specimens had been taken during the breeding season and that, in fact, the breeding grounds were not yet known. The birds referred to this race from Charleston, South Carolina, and from Sapelo Island off the coast of Georgia, were apparently all winter birds.

According to Chapman's account, there was much confusion regarding the birds of the south Atlantic Coast. Audubon's original specimen of *macgillivraii* (at least the bird on which his description was probably based) is in the U.S. National Museum (No. 2894) but without date or locality. It is a young bird in first plumage. Apparently most of the specimens from the south Atlantic Coast are of nonbreeding birds representing two or more subspecies. Ridgway considered that the winter birds taken at Corpus Christi and breeding specimens taken by E. A. MacIlhenny near Avery Island, Louisiana, were part of the same population of *macgil-*

livraii that Audubon described from Charleston, South Carolina, and that Audubon (1838) had said also occurred on the coast of Louisiana and Texas. The name *macgillivraii*, however, had already been synonymized with *maritimus* under the belief that the Charleston specimen was actually a *maritimus* bird in first plumage. Dr. Walter Faxon (1897) had tried to resolve the confusion by pointing out that since *peninsulæ* was the bird that was supposed to occur at Charleston, the name *macgillivraii* was applicable to *peninsulæ* and not to the Louisiana birds. Chapman (1899) then named the Louisiana birds *fisheri* in honor of Dr. A. K. Fisher, and he described the breeding range as from Grand Isle, Louisiana, westward probably to northeastern Texas. He stated that this race occurred in winter southward to Corpus Christi on the west and Tarpon Springs in the east. A color plate of *fisheri* and *sennetti* painted by Fuertes in 1898 accompanied Chapman's article.

The Ninth Supplement to the A.O.U. *Check-list* (1899) split *macgillivraii* into two races: *fisheri* of the Louisiana coast and *macgillivraii* restricted to the coast of South Carolina and Georgia. In the Third Edition (1910) of the A.O.U. *Check-list* (Fig. 1) the only additional changes were to put all Seaside Sparrows in the genus *Passerherbulus* and to assign the North Carolina birds to *macgillivraii*.

The Cape Sable Seaside Sparrow (*mirabilis*) was discovered by Arthur H. Howell (1919) in February 1918 at Cape Sable, where six specimens were collected. In assigning it full specific status Howell pointed out that the Cape Sable bird differs so strikingly from all other Seaside Sparrows that intergradation with any of the forms seems very improbable. In fact, it differed more from its nearest geographical neighbor (*peninsulæ*) than from other races of the species.

As pointed out by Oliver Austin in this symposium, Griscom and Nichols (1920) separated the Mississippi and Alabama birds from *fisheri* and gave them the name *howelli*, a name that persisted in the Fourth (1931) Edition of the A.O.U. *Check-list*. In the same paper, Griscom and Nichols assigned the name *juncicola* to the birds nesting on the Gulf Coast of Florida from St. Andrews Bay in Bay County east to southern Taylor County. These various changes were followed in the Fourth Edition (1931) of the A.O.U. *Check-list* (Fig. 1), which again changed the genus, this time to *Ammospiza*.

By the Fifth Edition (1957) of the A.O.U. *Check-list* (Fig. 1) the range of *maritima* had been expanded eastward and northward to include Martha's Vineyard, Cape Cod, and Plum Island, Massachusetts, and southward to include extreme northeastern North Carolina. *Macgillivraii* was considered to nest from Dare County, North Carolina, south to the Georgia-Florida line, and to include Oberholser's (1931) short-lived *waynei*, which Griscom (1944) determined was the light phase of *macgillivraii*. The range of *mirabilis* was shifted northward away from Cape Sable. *Peninsulæ* remained about the same, extending from Tampa Bay north to Lafayette County, Florida. *Juncicola* was considered to fill the entire gap between *peninsulæ* and *fisheri*, occurring from southern Taylor County, Florida, west to Escambia Bay. Following Griscom's (1944) determination that *howelli* was merely the light phase of *fisheri*, *howelli* was merged with *fisheri*, which now has the greatest range of any

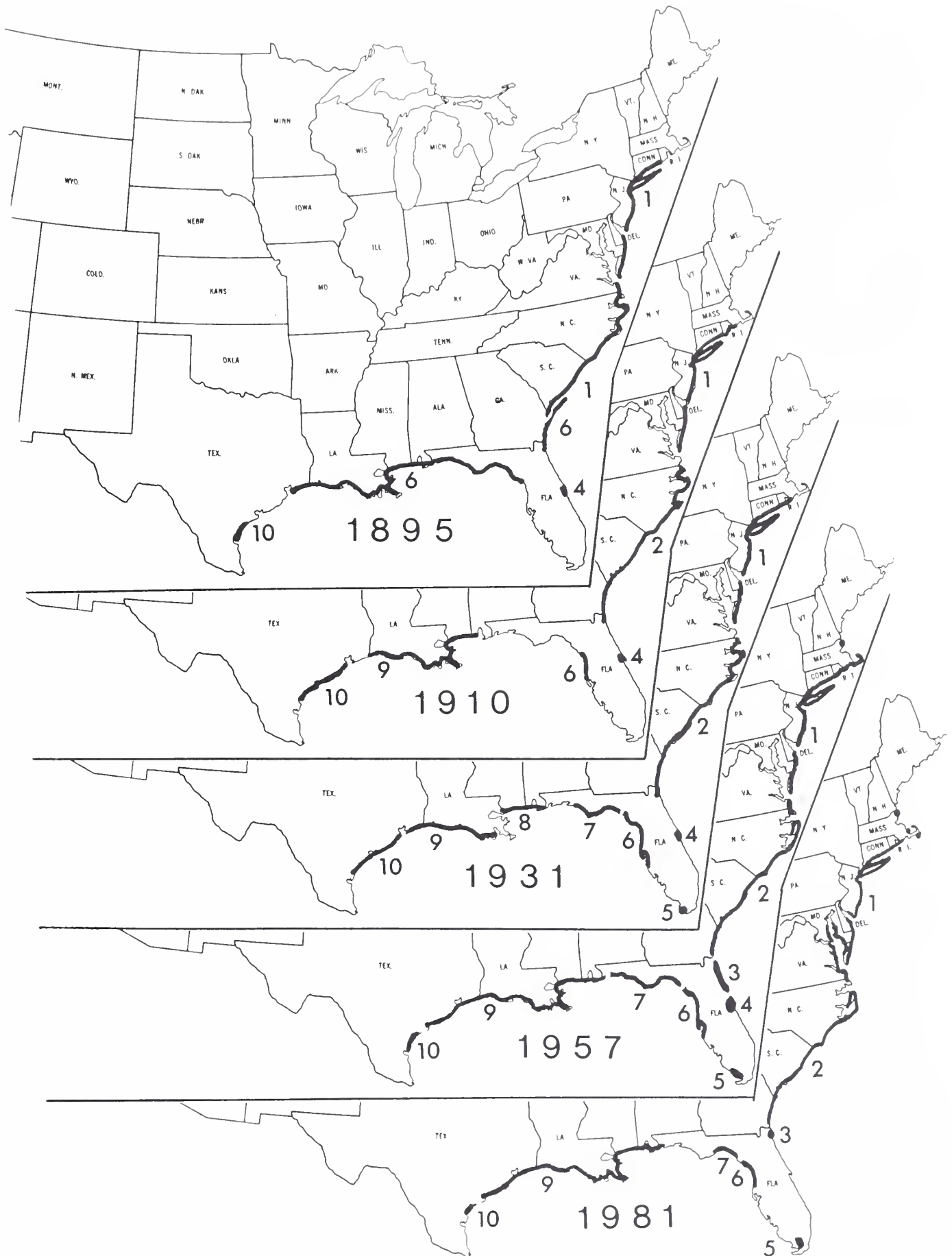


Fig. 1. Breeding ranges of the various subspecies of the Seaside Sparrow as summarized in the A.O.U. Check-list, Second Edition (1895) through Fifth Edition (1957), and approximate range in 1981. Subspecies are identified by number, as follows: 1 = *Ammodramos maritima maritima*, 2 = *A. m. macgillivraii*, 3 = *A. m. pelonota*, 4 = *A. m. nigrescens*, 5 = *A. m. mirabilis*, 6 = *A. m. peninsulae*, 7 = *A. m. juncicola*, 8 = *A. m. howelli*, 9 = *A. m. fisheri*, 10 = *A. m. sennetti*.

subspecies of Seaside Sparrow, occurring from Pensacola westward along the Gulf Coast to San Antonio Bay in Calhoun County, Texas. A new race, *pelonota*, described by Oberholser (1931) as occurring in northeastern Florida from Amelia Island in Nassau County south to New Smyrna in Volusia County filled a gap that had persisted on the northeast Florida coast.

Updating the ranges of the various populations of Seaside Sparrows for Bent's *Life Histories of North American Birds*, Austin (1968) and colleagues made the following additional adjustments in breeding range: The range of the Northern Seaside Sparrow, *maritima*, was expanded to include the shores of the Chesapeake Bay north to Idlewilde in Anne Arundel County, Maryland, and to Kent Narrows in Queen Annes County, Maryland. Its southern limit was extended to Elizabeth City in northeastern North Carolina. The Smyrna Seaside Sparrow, *pelonota*, was no longer found as far south as New Smyrna but only to Matanzas Inlet. There were no changes in the ranges of the other races.

Since that time, the breeding range of *pelonota* has been reduced to the marshes at the mouth of the St. Johns River, or perhaps to oblivion (see Kale, this symposium), and the entire wild population of *nigrescens* has disappeared. Some new populations of *mirabilis* have been discovered, expanding the range of that subspecies, but *peninsulae* has apparently abandoned all of Tampa Bay, and *juncicola* has lost more than half its original breeding range (Fig. 1).

Winter Range

The first attempt of the A.O.U. *Check-list* to describe winter ranges of Seaside Sparrows was in the Third Edition (1910). *Maritimus* was described as wintering from Virginia to Georgia; *fisheri* from Corpus Christi, Texas, to Tarpon Springs, Florida; and *macgillivraii*, strangely enough, was described as wintering along the Gulf Coast to Louisiana.

In the Fourth Edition (1931) *maritima* was changed to read from Virginia to northern Florida, rarely in Massachusetts, Connecticut, and New Jersey. *Fisheri* was claimed to winter southwestward along the coast to Corpus Christi, Texas, with no mention any more of birds moving eastward into Florida; but *howelli* was said to spread in winter to coasts of both northern Florida and Texas. The wintering of *macgillivraii* in Louisiana was deleted, and instead this subspecies was listed as only casual in winter on the Gulf Coast of Florida. The other races were assumed to be sedentary.

The Fifth Edition (1957) called for *maritima* to winter in coastal marshes from Virginia south to northeastern Florida (Amelia Island), occasionally north to New Haven, Connecticut, and to Plum Island, Massachusetts. *Macgillivraii*, *pelonota*, *peninsulae*, *juncicola*, *nigrescens*, and *mirabilis* were all stated to be resident. *Fisheri* was stated to winter south to Nueces County, Texas, and *sennetti* to the mouth of the Rio Grande.

In Bent's *Life Histories*, Austin (1968) expanded the winter range of *maritima* northward to include coastal and bay marshes from New York (Long Island) and Chesapeake Bay (Churchton) south to the previous southern limit. *Macgillivraii* was indicated as casual in winter south to northeastern Florida (St. Johns County). There were no changes in winter range of the other races.

PRESENT RANGE

Breeding

The present breeding range of the Seaside Sparrow can be described as a long, narrow series of disjunct populations occupying suitable salt- and brackish-marsh habitat along the Atlantic and Gulf Coasts from Plum Island in northeastern Massachusetts to Nueces and Copano Bays in southern Texas. Although primarily restricted to the coastal marshes and nearby bays, this species nests as much as 145 miles up Chesapeake Bay from its mouth.

Ranges of the various subspecies as presently known are as follows:

Ammospiza m. maritima. North to Plum Island, Barnstable, Monomoy, Dartmouth, and Westport, Massachusetts (unpublished data from Massachusetts Breeding Bird Atlas, courtesy of Richard Forster); tidal marshes of Rhode Island, Connecticut, and New York (primarily Long Island); New Jersey and Delaware, including Delaware Bay; the coasts of Maryland and Virginia, and tidal marshes of Chesapeake Bay and its tributaries north to Baltimore County (unpublished data, Baltimore County Breeding Bird Atlas, courtesy of Robert Ringler); and on the Eastern Shore of the Chesapeake north to Kent Island in Queen Annes County; and south to Princess Anne County, Virginia, on the North Carolina border. A detailed map of estimated breeding range in Chesapeake Bay is shown in Figure 2. Range in the southern portion of the Bay is based on unpublished field notes of H. H. Bailey, who charted distribution of marshes suitable for Clapper Rails in 1915; most of the same marshes would be suitable for nesting Seaside Sparrows. Data for the northern half of the Bay are from F. R. Scott, H. T. Armistead, the Somerset and Baltimore County Breeding Bird Atlases of the Maryland Ornithological Society, and the breeding range as mapped by Stewart and Robbins (1958), updated by more recent observations from members of the Maryland Ornithological Society.

A. m. macgillivraii. Coastal and brackish marshes from Dare County in northeastern North Carolina south into Camden County in extreme southeastern Georgia.

A. m. pelonota. Now restricted to the marshes at the mouth of St. Johns River in Duval County, Florida (Paul W. Sykes, pers. comm., August 1981); as far as is known, this is the only remaining Seaside Sparrow population on the entire east coast of Florida.

A. m. mirabilis. Restricted to inland marshes on the west side of the south tip of the Florida peninsula, north and northeast of Cape Sable, north to the vicinity of Ochopee.

A. m. peninsulae. From Port Richey in Pasco County, Florida, north to Pepperfish Keys in Dixie County, Florida.

A. m. juncicola. From southern Taylor County, Florida, northwest to Wakulla in Franklin County, Florida.

A. m. fisheri. From Pensacola in extreme western Florida westward through Alabama, Mississippi, Louisiana, and eastern and central Texas as far as San Antonio Bay in Calhoun County.

A. m. sennetti. Restricted to the tidal marshes of Nueces and Copano Bays in southern Texas.

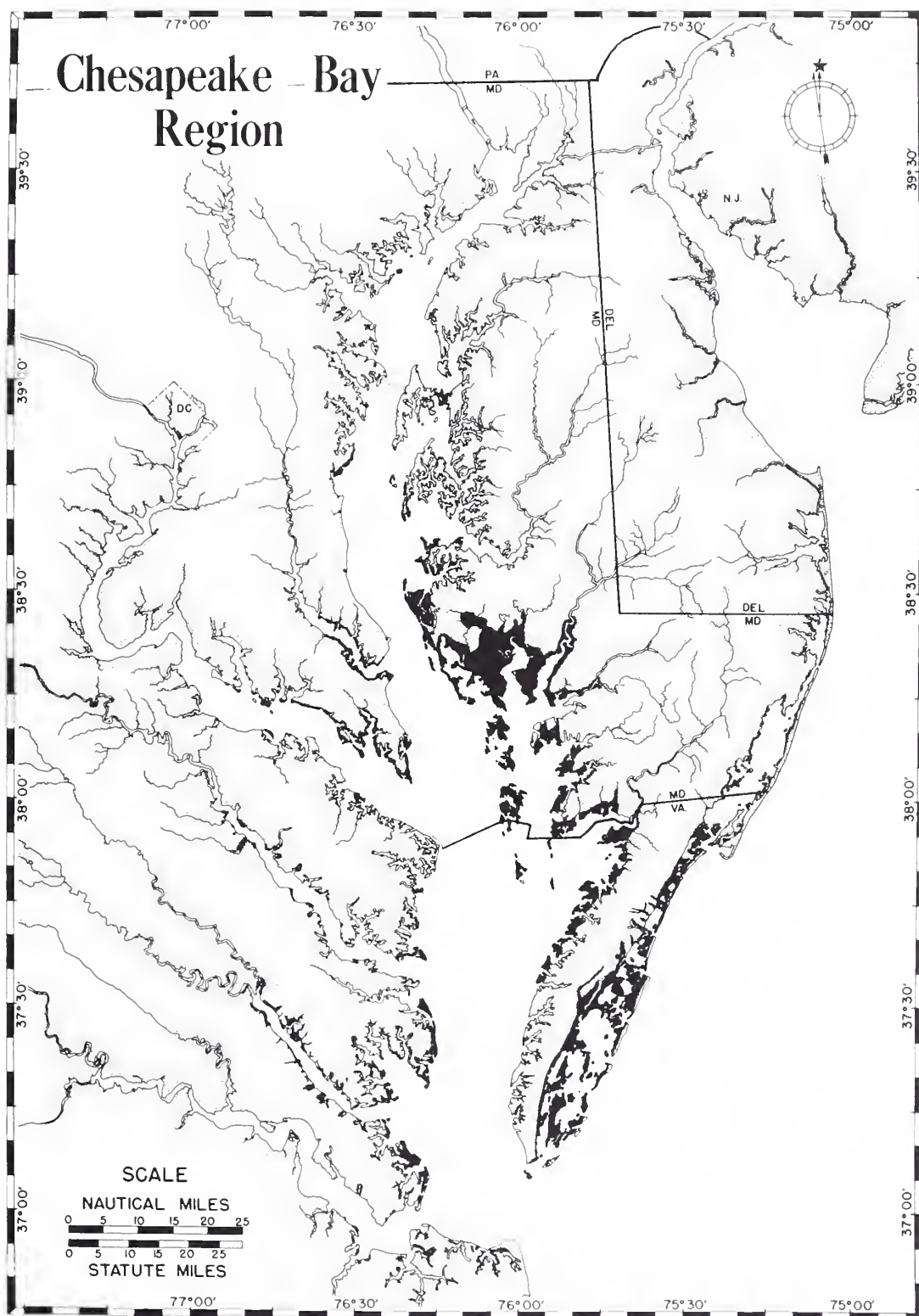


Fig. 2. Breeding distribution of the Seaside Sparrow in Chesapeake Bay.

Winter

Winter ranges are still poorly understood, partly because of the difficulty of identifying birds in the hand. Individual birds taken in the marshes of northwestern Florida have been identified as *juncicola*, *howelli*, *fisheri*, and *sennetti*, which Griscom (1944) indicated was highly unlikely; he concluded that all variations found in the region were no more than color phases of *fisheri*, which proves to be the most variable of all races. He stated that "The amount of individual variation in most subspecies is simply extraordinary, and its degree depends entirely on how many specimens have been collected, and how large the series amassed for study."

Quoting Oberholser (1974), "The Seaside Sparrow group is a difficult one, partly because nearly all the races have two well-marked color phases, which intergrade completely with each other and with the phases of other subspecies. The result is a somewhat bewildering aggregation of plumages. In attempting to sort these into subspecific order, it is necessary to make comparisons with individuals in corresponding phases. Even so, there frequently occur specimens that are difficult, or nearly impossible, to place subspecifically with certainty."

Maritima winters irregularly north to the coast of Massachusetts and some birds attempt to winter on Long Island each year. Marshes in the Chesapeake and ocean shores of Maryland regularly contain wintering Seaside Sparrows in milder winters, but few if any can be found after any prolonged freeze of the marshes. The same is true of the Chesapeake marshes of northeastern Virginia. The winter range of *maritima* is believed to extend south to northeastern Florida (Amelia Island), and possibly to Fort Pierce (Austin 1968).

Macgillivraii is considered primarily a permanent resident, but it has been found casually as far south as St. Johns County, Florida, in winter.

All of the Florida races are considered permanent residents, except that *fisheri*, the race that breeds from extreme western Florida to central Texas, has been recorded in winter south to Nueces County, Texas.

Sennetti has been recorded in winter as far south as the mouth of the Rio Grande, about 120 miles south of its breeding range.

POPULATIONS

Breeding Season

Breeding bird densities of *maritima* have been estimated at a dozen or more sites in New York, New Jersey, Delaware, and Maryland, and the results published in various issues of *American Birds* and its predecessor journals. By far the greatest density reported was 1999 pairs per km², based on 55 pairs in 6.8 acres of salt marsh at Oak Beach in Suffolk County, Long Island, New York by William Post (1970). Other densities of more than 100 pairs per km² (based on populations of 10 or more pairs), were recorded from salt-marsh habitats in New York and New Jersey by Imhof (1940, 1941), Enders (1967), Anes et al. (1966), and McDonald and Potter (1941). These plots ranged in size from 6 to 10 hectares, and (except in the one censused by Post) densities ranged from 131 to 214 singing males per km².

Seaside Sparrows have been recorded on 17 of the randomly distributed roadside routes of the Breeding Bird Survey (BBS). About 43% of the 637 Seaside Sparrows recorded on Breeding Bird Survey routes through the year 1979 were identified in Maryland, which not only has extensive marshes along the eastern shore of Chesapeake Bay but also has a high sampling density of BBS routes. The highest counts from the 50-stop BBS routes were 34 individuals on the Blocton, Alabama, route in 1977 and 33 individuals along the Madison, Maryland, route in 1973. In Delaware, where there is a high percentage of salt-marsh habitat available within the state, five of the ten BBS routes have reported this species two or more years. The mean numbers of birds per route give a rough indication of the proportion of suitable tidal marshland within each of the coastal states: New York, 0.003 birds per route; New Jersey, 0.040; Delaware, 0.587; Maryland, 0.379; North Carolina, 0.225; South Carolina, 0.050; Florida, 0.011, Alabama, 0.360; and Louisiana, 0.021. The sample size is too small to permit computation of population trends.

Winter Season

Relative abundance in winter, based on Audubon Christmas Bird Counts for 1977 through 1979, is indicated in Figure 3. The area of the dots is roughly proportional to the mean number of Seaside Sparrows reported per 10 hours of field work in salt-marsh habitats. Although Christmas Bird Count data may vary considerably from year to year, the 3-year means give a rough idea of some of the main concentration areas.

The highest counts, as many as 443 birds in 1980, came from the Sabine National Wildlife Refuge in southwestern Louisiana, closely followed by a tally of 161 birds in 1979 at nearby Johnsons Bayou. The greatest concentrations in Texas were reported from the vicinity of Houston. The only other Gulf Coast locality with a notable count was Cedar Key, Florida.

Atlantic Coast birds appear to be concentrated primarily from McClellanville, South Carolina, to St. Augustine, Florida. The Fort Pierce counts were exaggerated by the very small proportion of time (2%) spent in salt-marsh habitat. Seaside Sparrows have been found one or more winters on most of the coastal Christmas Bird Counts from Maryland north to Cape Cod, but numbers are small and very few localities record them every year.

MIGRATION

It is difficult to detect migration of the Seaside Sparrow, especially in the great majority of its geographic range that is occupied at all seasons of the year. Earliest dates of spring arrival range from a very early 14 April 1890 on Monomoy Island, Massachusetts, and 13 April 1929 in Smittstown, New York, to 28 April 1980 in New Haven, Connecticut. Late dates of spring departure from the wintering ground are 12 April 1936 from Ft. Myers, Florida, 18 April 1928 from Chatham, Georgia, and 6 May 1899 from Mount Pleasant, South Carolina.

Early dates for detection of fall arrival are 3 October 1909 at Savannah, Georgia, and 4 October 1936 at Ft. Myers, Florida. It is difficult to separate fall departure

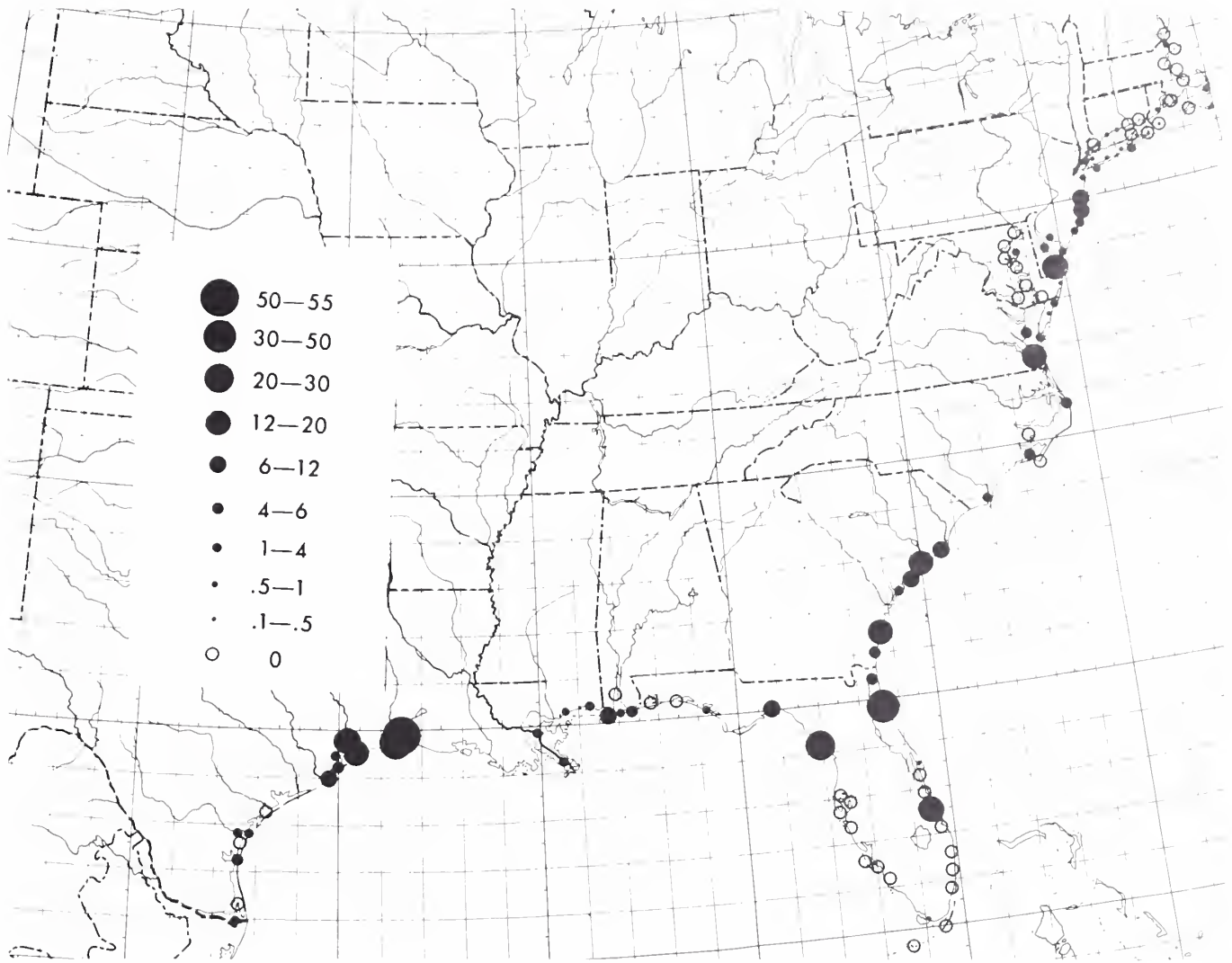


Fig. 3. Relative abundance of the Seaside Sparrow in late December based on the mean number of birds recorded per 10 party-hours of field work in salt-marsh habitats, 1977 through 1979.

dates from birds attempting to winter, but the following dates are said to be those of fall departure: 12 September 1953 from Martha's Vineyard, Massachusetts; 12 October 1912 from Quonochontaug, Rhode Island; 30 October 1889 from New Haven, Connecticut; 25 November 1885 from Far Rockaway, New York; and 25 November from Cape Henry, Virginia. All of the preceding dates are from Austin (1968) or the distribution and migration files of the U.S. Fish and Wildlife Service at the Patuxent Wildlife Research Center, Laurel, Maryland.

The median date of spring arrival at Fairfield, Connecticut, based on 30 years of records by A. A. Saunders, is 18 May; his median departure date, based on 11 years, is 19 September (distribution and migration files, U.S. Fish and Wildlife Service). Cruickshank (1942) records a spring peak in the New York City area during the third week in May, and stragglers still passing through up to the second week in June. He places the fall peak in the middle of October and says the migration is virtually concluded by the middle of November. Of 15 birds killed at television towers in the vicinity of Wilmington, North Carolina, from 1970 through 1972, 13 struck during the middle third of October and 6 during the final third of that month (Carter and Parnell 1976).

WANDERING

Nearly all observations of the Seaside Sparrow are remarkably restricted to within a few hundred meters of tidewater. Few North American birds are so strictly confined to such a narrow geographic range. The fact that portions of the range are especially vulnerable to effects of hurricanes makes it even more notable that there are almost no inland reports. Ever since 1949 the editors of *Audubon Field Notes* and its successor *American Birds* have made a practice of printing unusual occurrences in boldface type and indexing these observations for easy reference. It is significant that during this entire 32-year period not a single report of a Seaside Sparrow has been boldfaced.

For many decades a 2 October 1885 specimen from Ossining, on the Hudson River, New York, and an 18 August 1884 specimen from Shark Rock in Muscongus Bay, Maine, remained the sole records from north of the breeding range. During the past dozen years, however, it has become apparent that this species regularly wanders north to the coast of Maine after the breeding season (Peter Cannell, pers. comm.).

Until two decades ago the Seaside Sparrow was one of the few bird species whose range was entirely re-

stricted to the United States. Then, on 5 February 1962, one was taken in Halifax County, Nova Scotia. There are now no fewer than nine records for New Brunswick and seven for Nova Scotia, or an average of nearly one record per autumn from the coast of the Canadian Maritime Provinces in recent years. Summarizing those Maine, New Brunswick, and Nova Scotia reports for which I have succeeded in obtaining dates of first appearance, from the literature and from bird banding records, there are 10 for August, 5 for September, and 4 for October. Extreme dates (excluding the wintering bird from Nova Scotia) are 5 August to 24-26 October. Ten of the 19 autumn dates fall in the period 13 August to 1 September, indicating the period of peak occurrence. The two records in the files of the U.S. Fish and Wildlife Service of Seaside Sparrows striking lighthouses on Long Island at night also indicate movement in August: 20 August 1882 at Fire Island and 7 August 1888 at Little Gull Island.

In southern North Carolina, Carter and Parnell (1976) found that small numbers of migrating Seaside Sparrows regularly collided with guy wires at the 608-m tall WECT TV tower in Bladen County in October (1970-1972). This tower is about 80 km inland from Wrightsville Beach and suggests a substantial overland migration that had not previously been suspected. The only other inland TV tower casualty reported for this species was a female found on 5 November 1968 at the WRAL tower 14 km southeast of Raleigh, North Carolina, and identified by R. C. Laybourne as *A. m. maritima* (Post and Browne 1971).

The most recent inland sighting was 5 to 7 September 1981 at Concord, Massachusetts, by Walton (1981), the first inland record for New England.

Occasionally a spring migrant overshoots its breeding range. Vickery (1978) indicates that the Seaside Sparrow is rare on the coast of Maine from mid-May to early June, but he does not cite specific records. There have been five published reports from parks in New York City: three from Central Park in May, one from Prospect Park in May, and one from Van Cortlandt Park (Carleton 1958, Bull 1964). The most extraordinary spring strays were two reported from inland localities in Pennsylvania by Poole (1964). The first was a specimen in the Reading Museum labeled "Fritz's Island" near Reading, 30 April 1887. The second was a bird "taken in a banding trap at Berwyn some years ago and identified by Franklin L. Burns (*vide* Conway)." This bird was reported to the U.S. Fish and Wildlife Service by Burns as having been observed on 20 May 1941, but with no further details. Albert E. Conway (pers. comm., 25 September 1981) vouches for the identification, but I have been unable to find any record that the bird was banded and released; possibly it resides in some collection.

In the Gunpowder River area at the head of Chesapeake Bay, the Seaside Sparrow has been recorded in 3 years, between the extreme dates of 21 April and 10 June (Stewart and Robbins 1958), and there has been one spring sighting near the upper limit of tidewater in the Potomac River at Dyke Marsh in Fairfax County, Virginia (Scott and Cutler 1975).

Much remains to be learned about migration and wandering in the various populations of the Seaside Sparrow. With a few notable exceptions, banders have

made little effort to study this interesting species. As of August 1978 only 3,184 individuals had been reported banded, and as of August 1980 the Bird Banding Laboratory had only two records of movement by this species, both well verified. The first was banded as an immature at Fire Island, Long Island, New York, by D. B. Ford on 24 July 1977; 20 days later it was caught at Quonochontaug in Washington County, Rhode Island, by Douglas L. Kraus, an alert birder who noticed the band and pursued the rain-drenched bird until he caught it by hand. The second was banded as a local bird in or recently out of the nest at East Quogue, Long Island, by Leroy Wilcox on 21 June 1978 and retrapped on 29 August of the same year 40 miles to the west at Oak Beach, Long Island, by Will Post.

A carefully organized cooperative banding study of this species would greatly enhance our knowledge of the extent to which the various populations wander and migrate.

Griscom (1944) stated that 97% of the specimens of *maritima* cannot be distinguished from the intermediate phase of *macgillivraii* and that "final proof of the migration of *maritima* south into the range of *macgillivraii* will depend upon banding." He further stated, in reference to the Gulf Coast races, that "Nothing is to be gained by the further shooting of odd-looking birds in winter." I agree completely with Griscom that we must rely primarily on banding to determine which populations are migratory and to what extent.

THE FUTURE

In all parts of its range the Seaside Sparrow is being crowded out by loss of salt-marsh habitat, and I see no hope for a reversal of this trend within the foreseeable future. We are all familiar with the continued exploitation of Atlantic coastal marshes for housing, recreation, and other human activities. Even along the sparsely settled Texas coast the situation is disturbing, as summarized by Edgar Kincaid in Oberholser's *The Bird Life of Texas* (1974): "Since World War II much of this bird's saltmarsh habitat, formerly almost unbroken from Sabine Pass to Corpus Christi, has been developed out of existence. Smog-producing oil refineries, chemical plants, and hordes of automobiles continue to sprout like evil-smelling mushrooms."

It is my hope that this symposium will not only stimulate further research on this species, but that we can pinpoint strategically located areas of choice nesting habitat for each subspecies and take steps to see that sizable tracts are protected from further encroachment.

ACKNOWLEDGMENTS

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Distribution, Habitat, and Status of Breeding Seaside Sparrows in Florida

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Abstract. Six subspecies of the Seaside Sparrow (*Ammospiza maritima*) are resident in the coastal marshes of Florida: Smyrna Seaside Sparrow (*A. m. pelonota*), Dusky Seaside Sparrow (*A. m. nigrescens*), Cape Sable Sparrow (*A. m. mirabilis*), Scott's Seaside Sparrow (*A. m. peninsulae*), Wakulla Seaside Sparrow (*A. m. juncicola*), and the Louisiana Seaside Sparrow (*A. m. fisheri*). The Smyrna Seaside no longer breeds south of the St. Johns River in Duval County, and the abundant population north of the river is continuous with the Georgia population of MacGillivray's Seaside Sparrow (*A. m. macgillivrayi*) with which they are probably synonymous. The Dusky population is now represented by only five males held in captivity at the Sante Fe Community College Teaching Zoo in Gainesville. No birds remain in the historic range of this race located in northern Merritt Island and the St. Johns River valley of Brevard County. The Cape Sable Sparrow remains healthy with several thousand pairs in Everglades National Park and in the Big Cypress Preserve. Scott's Seaside, formerly found south to the Anclote River, occurs abundantly in *Juncus* marshes from Port Richey north to the Pepperfish Keys area of Dixie County where it merges with the Wakulla Seaside, also abundant in *Juncus-Spartina* marshes north to the Apalachee Bay area. Inexplicably, no breeding Seasides are found from Alligator Harbor west to Choctawhatchee Bay, where in the Hogtown Bayou marshes occur 50 to 75 pairs of a population that appears to be an intergrade of *juncicola* and *fisheri*. Three small populations of less than 200 pairs of the Louisiana Seaside occur in *Juncus* marshes in northeast Escambia Bay, the west side of East Bay, and the east side of Blackwater Bay, in Santa Rosa County.

Six subspecies of the Seaside Sparrow (*Ammospiza maritima*) are recognized by the A.O.U. *Check-list* (5th ed., 1957) as being resident in the coastal marshes of Florida (Fig. 1): the Smyrna Seaside Sparrow (*A. m. pelonota*), the Dusky Seaside (*A. m. nigrescens*), the Cape Sable Sparrow (*A. m. mirabilis*), the Scott's Seaside (*A. m. peninsulae*), the Wakulla Seaside (*A. m. juncicola*), and the Louisiana Seaside (*A. m. fisheri*). A seventh race, MacGillivray's Seaside (*A. m. macgillivrayi*), the resident population of the Carolina-Georgia coast, extends southward into northeast Florida. The nominate race, the Northern Seaside (*A. m. maritima*) occurs in winter from October through March on the Atlantic Coast regularly south to Ft. Pierce Inlet, St. Lucie County (Austin 1968, Kale and Pantelidis 1968) and occasionally south to the Miami area (Dade County) wherever extensive patches of Smooth, or Salt-marsh, Cordgrass (*Spartina alterniflora*) occur.

This paper reports on the results of surveys of these populations (excluding the endangered Dusky Seaside and Cape Sable Sparrows) conducted between 1975 and 1980. Surveys of the Dusky Seaside have been con-

ducted by personnel of the U.S. Fish and Wildlife Service since the early 1970s (Baker 1973), and in 1980 biologists from the Service, the Florida Game and Fresh Water Fish Commission, and Florida Audubon Society teamed up to make an intensive search of all potential Dusky habitat in the historic range of this sparrow (Delany et al. 1981) in the St. Johns River valley. Additionally, Sykes (1980) presented a summary of the status of the Dusky on Merritt Island. The Cape Sable Sparrow population has been surveyed annually since the mid-1970s by personnel of Everglades National Park and is the subject of two other papers in this symposium (Kushlan and Bass, Werner and Woolfenden, both this symposium; see also Kushlan et al. 1982). Hence, I will only briefly refer to the status of these two populations and devote most of this paper to the other five subspecies that breed in Florida.

METHODS AND STUDY AREAS

Each Seaside Sparrow population was surveyed similarly during the breeding season. Areas that could not be reached by road were surveyed on foot, but most

Seaside habitats were surveyed with a 16-foot flat-bottomed boat equipped with a 15-hp engine, or occasionally, a 6-hp engine. I would travel by car to a convenient boat ramp, then travel by boat 15 to 20 miles north and south (or east and west as the case may be) of this site. Intensity of coverage of habitats along the coast varied depending on access, tidal conditions, and water depths. For example, all work on the northeast coast was from the Intracoastal Waterway and all potential Seaside Sparrow habitat was easily reached for survey. Because the Intracoastal Waterway does not exist on the Gulf Coast between Tampa Bay and Apalachicola Bay, marshes along this coast, especially between New Port Richey (Pasco County) and Waccasassa Bay (Citrus County) can be reached only at high tide, and in some locations even this is with difficulty. Occasionally, I had to walk the boat into or out of the marsh for a distance of a half mile or more in the Gulf before water depth permitted use of the engine.

Access to the marsh at several Gulf Coast areas involved using a ramp located several miles inland on a river (Crystal, Waccasassa, Steinhatchee, and Econofina Rivers). The inconvenience and lost time that this may have incurred was more than offset by the incredible beauty and peacefulness of these forested, slow-moving coastal rivers.

Indispensable aids in the survey of Florida's coastal marshes are nautical charts (produced by the National Ocean Survey, formerly Coast and Geodetic Survey) and Florida Department of Transportation county road maps. Surprisingly, more detail concerning marsh features and place names appear on the D.O.T. maps than on the coastal charts. Surveyors working coastal marshes must have both. Another invaluable aid is a fiberglass bicycle flagstaff—the type used by bicyclists to make themselves visible to motorists. Anyone who has ever lost his boat in marshes that stretch for miles in all directions will never again leave it without inserting a reassuring flag into the marsh bed nearby.

Because of the vast expanse of coastal marsh between New Port Richey and Apalachee Bay, it was not possible for me to cover all potential Seaside Sparrow habitat. In some instances extremely shallow water at low tide prevented access; in others, distance from the nearest ramp put some areas beyond reach of a small boat. Occasionally, appearance of thunderstorms, always hazardous on open water and marsh, aborted some coverage (and in a few instances hastened my aging process).

In conducting the survey my usual procedure was to move the boat every quarter mile or so, shut off the engine, and listen and watch for singing males. If none were heard, I would emit a *pish-pish* sound until birds responded. If it is not too windy, Seasides, when present, always respond to “pishing,” or similar sounds, especially during the breeding season. Oftentimes, the sound of the outboard engine alone would stimulate song. Surveys were usually conducted over a period of several hours before and after high tide, hence I was able to travel most of the main tidal distributaries in the marsh system.

With experience one learns to recognize “suitable” Seaside Sparrow habitat, and within several minutes elicit a response from a resident sparrow if one is pres-

ent. Suitable or potential Seaside habitat varies somewhat depending on location along the coast. Extensive stretches of marsh grasses—either *Spartina alterniflora* or Black Needlerush (*Juncus roemerianus*) 3 feet or more in height and several hundred yards or more away from the mainland or any large tree-covered island — are prime habitat, with one exception, on both coasts. That one exception is the large pockets of *Juncus* that occasionally occur 1 or 2 miles inland from the Gulf Coast. These are invariably devoid of sparrows, at least in the breeding season. Two additional requirements are that the upper portions of the grasses must not be overtopped by normal high tides and a portion or most of the marsh floor must be exposed at low tide. Unlike Seasides in most of the other populations, the sparrows along the Gulf Coast from Port Richey north to Waccasassa Bay tolerate the invasion of numerous mangroves into their marsh habitat.

In May and June of 1975, I surveyed the Atlantic coastal marshes from Mosquito Lagoon, Volusia County, northward to Cumberland Island, Camden County, Georgia. In June 1976, marshes in St. Johns County, from Matanzas Inlet northward to St. Augustine were resurveyed, and in August 1981 the Mayport marshes south of the St. Johns River in Duval County were revisited. Surveys of the Gulf coastal marshes were conducted in June and July of 1979 and 1980.

RESULTS AND DISCUSSION

Smyrna Seaside Sparrow

Despite searches throughout all marsh-grass dominated habitats from Mosquito Lagoon north to the St. Johns River where it cuts across Duval County from west to east and empties into the Atlantic Ocean, no Smyrna Seaside Sparrows (*A. m. pelonota*) were found in the spring and summer of 1975. Searches in 1975 and again in June 1976 in the extensive *Spartina-Juncus* marshes between Matanzas Inlet and the St. Johns River again failed to locate any Seasides.

The history of the distribution of this population is an interesting one. When D. J. Nicholson (1946) first found them in 1922 at New Smyrna, Volusia County, he thought they were Dusky Seaside Sparrows. Several years later after some specimens were collected, Howell identified these as *A. m. macgillivraii* (Nicholson 1946). Nicholson (1928) reported scattered colonies from New Smyrna north almost to Daytona, a distance of about 10 miles, and colonies at Matanzas Inlet, 40 miles farther north.

In 1931, Oberholser described this northeast Florida population as the Smyrna Seaside (*A. m. pelonota*) and indicated its range to be from Nassau County to New Smyrna. His justification for describing this race as one separate from MacGillivray's Seaside, which it most closely resembles, was the existence of his newly described subspecies on the Georgia coast, *A. m. waynei*, which possessed in his opinion a lighter-colored plumage than did either the population along the Carolina coast or the northeast Florida coast (Oberholser 1931). In a second revision of the Seaside Sparrows in 1944, Griscom (1944), chiefly on the basis of Ivan Tomkins's Georgia field studies (Tomkins 1937), rejected *waynei* as being only a light phase of *macgillivraii*, but

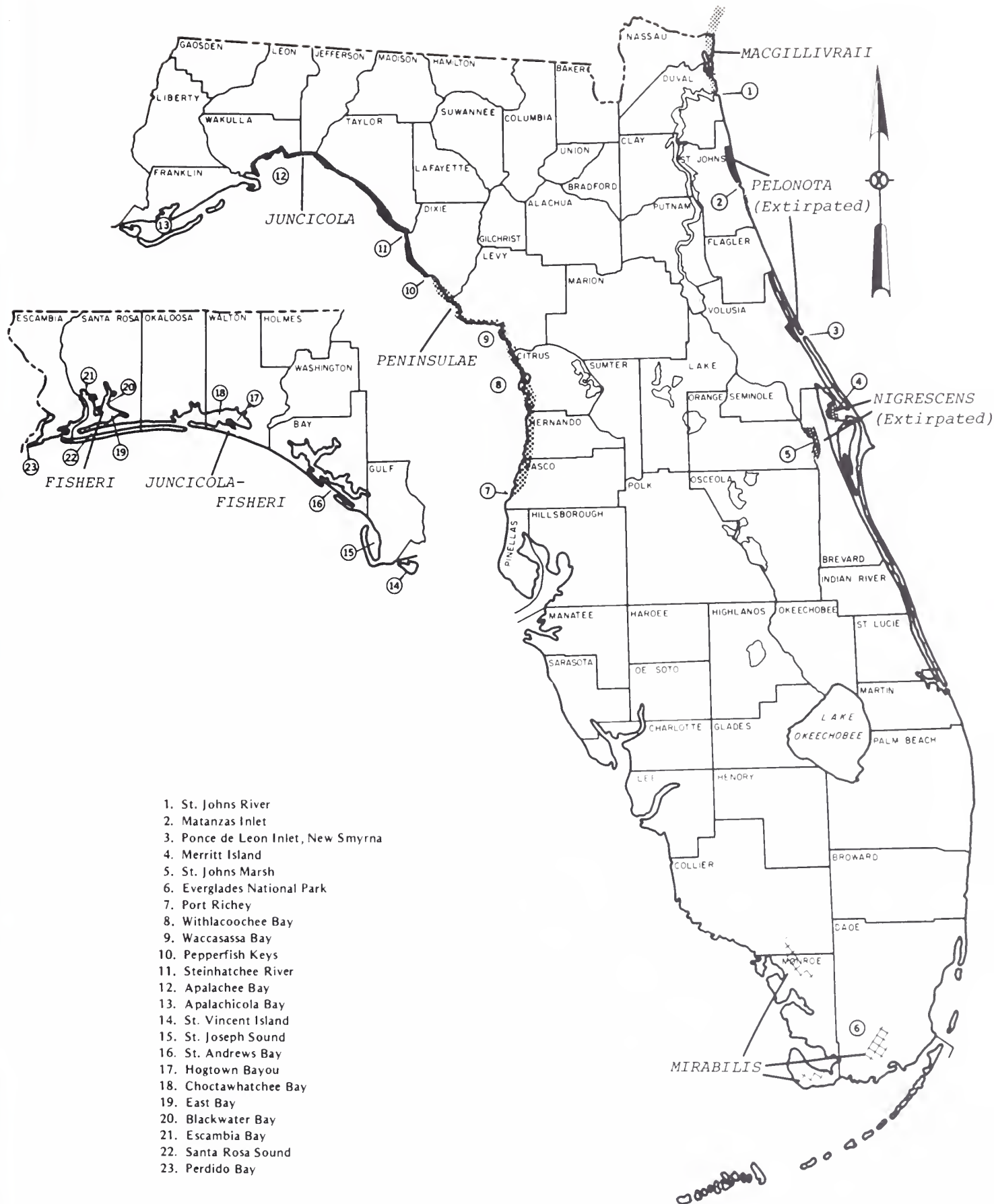


Fig. 1. Present distribution of the Seaside Sparrows (*Ammodramos maritima*) in Florida, including the former range of the extirpated populations of *A. m. nigrescens* and *pelonota*. The recently discovered population in Choctawhatchee Bay (Walton County) appears to be an intergrade between *A. m. juncicola* and *fisheri*. The three colonies of *fisheri* are indicated by the three black dots in Santa Rosa County.

he accepted *pelonota* "as a barely recognizable minor population in northeast Florida," and added, "but I doubt if its range should be extended north to the northern end of Amelia Island." Although the A.O.U. Check-list committee also refused to accept *waynei*, it retained the political boundary between Georgia and Florida as the biological boundary between the subspecies *pelonota* and *macgillivraii*.

Nicholson (1928) described the New Smyrna habitat of this population as follows: "At this point the river is very wide, perhaps three-quarters of a mile. There are many islands coursed with shallow sloughs and mudflats exposed at low tide. Some are covered with dense growths of *Salicornia* [See comment below.—HWK] mixed with marsh grass and fringed with mangrove trees and here and there among the open spots are small mangroves several feet high surrounded by the undergrowth."

At this point I must correct an error in plant identification made by Nicholson and repeated by every subsequent author who has quoted him. Nicholson repeatedly mentions "*Salicornia*" and "matted *Salicornia*." Although *Salicornia* is commonly present in the salt marsh, the plant Nicholson was referring to is Saltwort or Pickleweed, *Batis maritima*, a common low, woody succulent that grows in extensive mats in the natural mangrove scrub throughout the subtropical coastal marsh. A photograph of a "nest and four eggs in *Salicornia*" in Figure 6 on page 231 of Nicholson's 1928 paper clearly is that of *Batis maritima*.

In 1946 Nicholson reported "... of recent years the marsh has ... filled with great numbers of mangrove bushes, and trees now have grown to considerable size" (Nicholson 1946). In 1950, he wrote "as recent as 1939, hundreds of birds still bred in this marsh, but since that date have become increasingly fewer in number, and during the springs of 1948 and 1949 ... not a single bird ... was in evidence" (Nicholson 1950). He concluded that the northward advancing mangrove had displaced the Seaside's preferred open grassy marshes.

Austin (1968) felt that a more likely cause of their disappearance was the heavy spraying with DDT for mosquito control in the late 1940s and early 1950s, although he presented no evidence to support this. I disagree with this speculation, however, because the Seasides were already gone by the time DDT came into extensive use in these marshes. Today, both Red Mangroves (*Rhizophora mangle*) and Black Mangroves (*Avicennia germinans*) extend abundantly north to Matanzas Inlet, and in scattered patches north to St. Augustine. In 1975, I found the northernmost limit of Black Mangrove to be about a half mile north of St. Augustine along the Intracoastal Waterway (ICW). In December 1981 I was again on the ICW north of St. Augustine and noted that in the interval of only 6 years (and despite three winters with killing frosts) the mangrove had advanced another 2 miles farther northward.

Two species of birds commonly associated with mature mangrove habitat—the Black-whiskered Vireo (*Vireo altiloquus*) and Gray Kingbird (*Tyrannus dominicensis*)—have also extended their range northward, and in 1975 both species were abundant in the mangrove habitat of New Smyrna. No vireos were found north of Daytona Beach, but the kingbird occurred

sparsely along the ICW as far north as St. Augustine. Hard freezes in the winters of 1977 and 1979 killed back many mangroves, and these have been slow to recover to their original height. One result is that on 16 May 1981 I did not see or hear a single Black-whiskered Vireo in the New Smyrna marshes where in 1975 dozens of birds were heard singing.

Nicholson (1950) also mentioned that the changed character of the marsh had driven out the resident Long-billed Marsh Wren (*Cistothorus palustris griseus*) and had greatly reduced the Clapper Rail (*Rallus longirostris*) population. As with the Seasides, I did not find any breeding wrens south of the St. Johns River, but Clapper Rails were abundant in both mangrove-*Batis* marshes at New Smyrna and throughout the marshes northward. Migrating Northern Marsh Wrens (*C. p. palustris*) were noted on 14 May in the *Juncus* marshes of Spruce Creek, just north of New Smyrna, and one Wayne's Marsh Wren (*C. p. waynei*) was collected on 22 May in the short *Juncus-Spartina* marsh just south of Matanzas Inlet.

Patches of *Spartina-Batis* marsh surrounded by Black and Red Mangroves still exist in the New Smyrna area, but these apparently are too small in size to attract breeding Seaside Sparrows or Long-billed Marsh Wrens, although in winter both species occur there.

Trost and Austin (Austin 1968) found Seasides breeding in marshes along the Matanzas River (ICW) from Matanzas Inlet north to the Crescent Beach area in 1959, and birds collected there in September 1963, April 1964, and October 1966 (FSM collection) suggested breeding may still have been occurring in those years. In the late 1960s, George A. Watson (pers. comm.) collected Seasides in this same area, hence the disappearance of the Seaside Sparrow (and the Long-billed Marsh Wren) from this part of the range is of recent occurrence. The reason or reasons for the extirpation of these species north of Matanzas Inlet is unknown. North of the inlet mangroves occur only in scattered patches, and vast stretches of open *Spartina* marsh still remain. Relatively little disturbance of marshlands by man has occurred along this part of the coast. In winter these marshes continue to support large populations of overwintering Seasides, Long-billed Marsh Wrens, and Sharp-tailed Sparrows (*Ammodramus caudacuta*). I do not know what the grass height was in these marshes in the past, but my overall impression (and I must emphasize that it is an impression only) of the present grass height in much of the area south of the St. Johns River is that it is too short for safe nesting above high tide.

Beginning about a half mile north of the St. Johns River in Duval County, both Seaside Sparrows and Long-billed Marsh Wrens occur abundantly in the *Spartina* marshes along the ICW northward into Georgia. They did not occur within 300 to 650 feet of large wooded islands, and were not found in the marshes between Little and Big Talbot Islands, nor in the marsh close to Ft. George Island, probably for this reason. Otherwise the marsh near these islands appears to be suitable habitat.

Westward of the ICW a series of tidal creeks occurs on the north side of the St. Johns River. All of these creeks are interconnected, but only two of them—Cedar

Point and Clapboard—open directly into the St. Johns. Seasides were found in Sisters Creek (= ICW), Hannah Mills Creek, and Cedar Point Creek, but not in the more westerly Clapboard Creek or any of the other creeks west of Clapboard. The *Spartina* marshes for several miles north of the St. Johns contain scattered patches of *Juncus*, also occupied by Seasides, but farther northward, *Juncus* is restricted to the fringes of higher islands and the mainland and no Seasides inhabit these fringes.

The *Spartina* marshes of Nassau County continue northward without break, except for numerous rivers and creeks, into Cumberland Sound and the Camden County marshes of Georgia. Seaside Sparrows occurred in all of this marsh. No Seasides were found in marshes extending up into the valleys of rivers entering the sounds from the mainland, even where broad extensive marshes were present. Marsh wrens did occur farther up the river, but never more than about a mile from the open sounds.

A crude estimate of the breeding population of Seaside Sparrows between the St. Johns River and Cumberland Sound, a distance of about 9 miles, is 1,000 pairs.

Though I have not yet completed my analysis of Georgia and Florida specimen material in museum collections throughout the United States, to date I have detected no plumage or mensural differences between specimens collected north or south of the Georgia-Florida line, and feel confident that the Seasides breeding in the Duval and Nassau marshes are *A. m. macgillivraii*. The population that once bred from New Smyrna north to Matanzas Inlet and St. Augustine is now extirpated, and if *A. m. pelonota* was indeed a valid, distinct population, then this subspecies is now apparently extinct.

Dusky Seaside Sparrow

The Dusky Seaside Sparrow (*A. m. nigrescens*), found only within Brevard County, Florida, is the most distinctive of all the Seasides because of its striking black-and-white streaked pattern. It was once considered to be a separate species, but in 1973 it was reduced to subspecific status by the A.O.U. Check-list Committee (Eisenmann 1973). In all respects it is a typical Seaside Sparrow and its relegation to subspecific status was justified from a biological and taxonomic viewpoint, but in terms of the conservation of the population, this action dealt it a blow that has hastened it along the road to extinction. Because the Dusky had become merely a subspecies, it received less attention and lower funding priorities from both state and federal agencies, and at the same time lost the popular appeal and status that a rare species is accorded by the evergrowing bird-watching public. Thus, at a critical time in its evolution, the Dusky Seaside Sparrow lost its human constituency, which is the *only* force that state and federal wildlife agencies will respond to. Sykes' (1980) paper on the decline and disappearance of the Dusky from Merritt Island presents a clear picture of the causes for the extirpation of this population from Merritt Island. From a high of probably 2,000 or more pairs in the first half of this century, it is now extirpated—in part possibly a result of pesticide use in

the 1940s and early 1950s (Nicholson, in Austin 1968), but primarily because of destruction of its marsh-grass habitat by impounding of the marsh for control of mosquito breeding in the 1950s and 1960s.

In the St. Johns marshes, from State Road 46 in northern Brevard County, south to SR 520 in central Brevard, its historic range in the valley, Brian Sharp (1970) estimated a population of between 530 and 829 males in 1968. Commendable efforts by the U.S. Fish and Wildlife Service to purchase refuge lands for the Dusky were offset by insufficient funding and bureaucratic ineptitude that resulted in continued overdrainage of habitat (initiated in the 1920s but accelerated in the 1960s), and extensive wildfires that destroyed all but a handful of birds in the mid-1970s. By 1978 only 24 birds remained; this number dropped to 13 in 1979, and to 6 (all males) in 1980. All but one of these surviving males were captured in July 1980 and brought into captivity in Gainesville, Florida, for safekeeping. Searches for surviving wild males in 1981 and 1982 have failed to find any. A full report on the 1980 and 1981 surveys appears in Delany et al. (1981).

Hence, the current status of the Dusky Seaside Sparrow is represented by five aging (ranging from 6 to 9 years of age) captive males. With an interest in preserving the surviving Dusky gene pool in living birds, the Department of Interior's Dusky Seaside Sparrow Recovery Team and biologists and conservationists from throughout the United States recommended breeding these males with females from the dark-colored Florida Gulf Coast population, with subsequent backcrossings with the parental males. Initially, the U.S. Fish and Wildlife Service refused to permit such a project (see James 1980), but in 1982, after a 2-year delay, the Service granted approval to breed the Dusks in captivity with the proviso that no federal funds could be expended on the project. If this breeding project, now under way, is not successful in reconstituting a viable population, the Dusky Seaside Sparrow will become extinct with the passing of these five captive males.

Cape Sable Sparrow

This extreme southern Florida subspecies (*A. m. mirabilis*) was also once considered a separate species, but as Griscom wrote in 1944, it "has no real claim to specific distinctness. It has a small local population in an extreme development of the light phase. While it is the greenest of the Seaside Sparrows, duller specimens can not be distinguished above from the most olive *sennetti* . . ." of the southern Texas coast population. It is the most isolated geographically of all the Seasides and the only one to demonstrate in modern times the role of hurricanes in the evolution of populations. The 1935 hurricane that swept over Cape Sable destroyed practically all of the Cordgrass habitat and probably most of the birds (Stimson 1956).

According to Kushlan and Bass (this symposium), an estimated 1,500 to 2,000 pairs of Cape Sable Sparrows occur in four major sites: Taylor Slough and the east Everglades, Cape Sable, Ochopee, and the Big Cypress. Except for portions of the East Everglades and the Ochopee area, most of these sparrows occur on lands under jurisdiction of the Everglades National Park. A management plan for this population has now

been developed by the National Park Service (Kushlan et al. 1982).

Scott's Seaside Sparrow

The A.O.U. *Check-list* (5th ed.) states that this race (*A. m. peninsulae*) is resident on the Gulf Coast from Pepperfish Key (Dixie County) to Old Tampa Bay (Hillsborough County). Howell (1932) also mentions Old Tampa Bay, but Stevenson (in *litt.*) informs me that the only evidence for Scott's contention that Seasides nested south to Pinellas or Hillsborough County is that of a juvenile Seaside he collected in July. Thus, the historic distribution of this population was south to the mouth of the Anclote River where remnants of *Juncus* marsh still exist today.

In 1965 I found Scott's Seaside Sparrows and Marian's Marsh Wrens (*C. p. marianae*) breeding in extensive grass marshes fringed and dissected by Red Mangroves and Black Mangroves growing along mosquito-control drainage ditches along Green Key Road west of New Port Richey, Pasco County. The severe freeze of the winter of 1962-1963 had killed back most of the mangroves and by 1965 the vegetation still had not recovered its former growth. By 1979 mangroves had spread throughout most of this marsh and neither species of bird was present. I did not find any sparrows or wrens until Pound Net Creek, about 2.5 miles north of Green Key, and just northwest of Port Richey. Here, both species were singing in mangroves 13 to 20 feet high and in thickets of shorter trees near open patches of *Juncus*.

For someone intimately familiar with Seaside Sparrows and Long-billed Marsh Wrens of the east coast where a respectable bird would not even approach such a jungle of trees, let alone sing and breed in them, it was with an Alice-in-Wonderland feeling that I pushed my way through thickets and stumbled over the prop roots of 6- to 7-foot-high mangroves in an effort to see a marsh wren or a Seaside Sparrow singing within 3 to 6 feet of me. In the top of one mangrove a Seaside Sparrow was singing, and just below him, almost 13 feet above the marsh bed, was the courtship nest of a marsh wren. Apparently, so long as numerous patches of *Juncus* are interspersed throughout the area, the sparrows and wrens will tolerate this invasion of their marsh habitat by mangroves. When the thickets of mangroves become too extensive, as they have farther south, these grassland birds move out. The absence of sparrows and wrens from some apparently similar sites as I moved northward suggests that this exclusion process is already occurring in this region. Seaside Sparrows are sparse along the edge of the Gulf between Hudson in Pasco County and the Suncoast Keys near the mouth of the Homosassa River in Citrus County. Much of the habitat is low-growing mangrove, scattered *Juncus*, surrounded by extremely shallow water with numerous islets and limestone shoals. Seasides may reside in some of the extensive *Juncus* marshes up to a mile or so from the mangrove-fringed Gulf, but I was not able to reach these from either the landward or the seaward side. The fact that marsh wrens were present in much of the area I covered suggests that Seasides were indeed scarce.

Seasides again became numerous north of Homosassa in the extensive Salt River marshes and at Fort

Island west of Crystal River. From here northward, mangroves no longer dominate the outer marshes or islands and every mile of marsh contained breeding Seasides and marsh wrens. *Spartina alterniflora* began to appear as an outer fringe of the *Juncus*, interspersed with patches of *Distichlis*. Along much of the Gulf Coast north of Withlacoochee Bay, the Seaside Sparrow truly lives up to its name. Every grass-covered island, an acre or more in size, and every point of marsh jutting out into the Gulf is home for one or more pairs of Seasides.

North of Cedar Keys, Levy County, only an occasional mangrove occurred, and on Pepperfish Keys, off the coast of Dixie County, the northern boundary of Scott's Seaside, the white skeletons of dead mangroves stood as silent reminders of the killing frosts that limit the spread of mangroves farther northward. Male Seasides used the occasional small dead trees as song perches.

Because not all possible Seaside Sparrow habitats were actually visited along several areas of the Gulf, especially south of Crystal River, my figure for the population size of Scott's Seaside Sparrow between Port Richey and Pepperfish Keys is extremely crude, but conservatively, I estimated between 2,500 and 3,500 pairs.

Wakulla Seaside Sparrow

The A.O.U. *Check-list* suggests a gap of several miles between *A. m. peninsulae* and *A. m. juncicola*, with the former extending northward to Pepperfish Keys and the latter southward to southern Taylor County (the Steinhatchee River), although Howell (1932) acknowledged that the two races intergraded in southern Taylor County. Plumages of Seasides I collected in the marshes on the mainland east of the Pepperfish Keys in September 1979 were rich in dark brown and black colors—probably the most beautiful of all the races, if that adjective can be applied to any Seaside. If one had to assign a particular specimen to one or the other subspecies, these would be determined as *juncicola*. I have just begun my study of museum specimens of the Gulf Coast races of Seasides, hence my impressions at this stage are tentative. Although differences between birds from opposite ends of the distribution of *peninsulae* and *juncicola* appear to exist, I feel that these are clinal and the designation of separate subspecies for adjacent and overlapping populations is not really justified.

In 1980 I found *A. m. juncicola* abundant in the *Juncus-Spartina* marshes of Taylor, Jefferson, and Wakulla Counties, westward to Piney Island, Porter Island, and Ochlockonee Point in western Apalachee Bay (Oysterbay). Griscom (1944) noted that "a real lacuna in our knowledge of Seaside Sparrows exists in northwestern Florida between Pensacola and Wakulla County." In June of 1980 I found no Seasides in Ochlockonee Bay, the marshes of St. James Island, Alligator Harbor, Dog Island, St. George Island, the extensive marshes south of Carabelle, or in the vast, mostly freshwater marshes of East Bay, at the head of Apalachicola Bay. Marsh wrens were abundant in Cat-tails growing in the East Bay marshes.

Although Howell (1932) found *A. m. juncicola* fairly common on the bay side of St. Vincent Island, I found

none there on 17 June 1980, nor were any marsh wrens heard. The habitat of mixed *Juncus* and *Spartina* appears to be ideal sparrow and wren habitat, and the absence of these species is a mystery. No Seaside Sparrows were seen in the scattered marshes of St. Josephs Sound.

Howell collected two singing male Seaside Sparrows in St. Andrew Bay, Bay County, south of Panama City in 1926, which he called *juncicola* (Howell 1932), but I found none there in 1980, nor were any found in nearby East and West Bays. The largest marsh in West Bay was diked and impounded in the late 1970s.

The A.O.U. Check-list indicates that *A. m. juncicola* occurs westward to Escambia Bay. This was based on misidentification of Howell's specimens taken there in 1936. Griscom (1944) in his revision of the Seaside Sparrows decided that these were Louisiana Seaside Sparrows (*A. m. fisheri*), not *juncicola*, hence the westernmost record for *juncicola* appears to be the two Howell collected in St. Andrew Bay.

No breeding Seaside Sparrows had ever been reported for Choctawhatchee Bay until 16 June 1980 when I found an estimated 50 to 65 pairs nesting in the *Juncus-Spartina* marshes of Hogtown Bayou, on the south side of the bay north of the town of Santa Rosa Beach, Walton County. Specimens collected then, and on 6 September 1980 and 10 October 1981, appear to more closely resemble *A. m. juncicola*, or an intergrade between *juncicola* and the dark phase of *fisheri* (see Griscom 1944). Interestingly, this is the only place in the course of my surveys in Florida where Seaside Sparrows were present, but marsh wrens were not.

Louisiana Seaside Sparrow

In 1933, Francis Weston (1965) discovered a large breeding colony of *A. m. fisheri* near Mulat in upper Escambia Bay, Santa Rosa County. Although the construction of Interstate Highway 10 in the early 1970s destroyed nearly a third of this *Juncus* marsh, I found a small colony of not more than 50 pairs in the marsh north of the Interstate in May 1980. About 6 miles away in East Bay, on the southeast side of the Avalon peninsula, which divides Escambia and East Bays, is an extensive (1,100+ acres) *Juncus* marsh. Here in 1979 and 1980 I found an estimated 100 pairs of Seaside Sparrows between Garcon Point and White Point.

On 11 October 1981 I also found Seaside Sparrows present in the extensive *Juncus* marshes on the east side of Blackwater Bay in the Catfish Basin-Weaver River area. Though this site was not checked during the breeding season, the expanse and quality of habitat suggest that breeding probably occurs here also.

In the 1930s Weston also found breeding Seaside Sparrows in other and smaller marsh areas at several points around Escambia Bay, including a small marsh island within Pensacola. A thorough search of these areas and also Santa Rosa Sound and Perdido Bay in May 1979 failed to find any Seaside Sparrows.

Sparrows collected in fresh plumage in September of 1980 and October 1981 are typical of dark forms of *A. m. fisheri*, as described by Griscom (1944). I estimated a total of approximately 200 pairs of *fisheri* in the three locations in Escambia Bay, East Bay, and Blackwater Bay.

Official Status on Florida and Federal Lists

The Dusky Seaside and Cape Sable Sparrows appear on both state and federal lists as endangered populations. The current population status of the Cape Sable Sparrow, coupled with the fact that most of its population occurs within the confines of Everglades National Park or the Big Cypress Preserve, would justify its being downgraded to threatened status.

Scott's Seaside (*A. m. peninsulae*) and the Wakulla Seaside (*A. m. juncicola*) are listed by the Florida Game and Fresh Water Fish Commission as Species of Special Concern because they inhabit wetlands that until recently, at least, were being drained and altered for development in many areas. Because the Santa Rosa County populations of the Louisiana Seaside (*A. m. fisheri*) are peripheral populations of a subspecies that extends westward to Texas, the Game Commission deleted this race from its list, unjustifiably in my opinion because the current status of *fisheri* throughout its range is not adequately known, and the underlying logic for Species of Special Concern status assigned to the other Florida populations, i.e. potential loss of wetland habitat, also applies to *fisheri* in Escambia, East, and Blackwater Bays. The Florida Committee on Rare and Endangered Plants and Animals (FCREPA), composed of biologists throughout Florida, considered *fisheri* to be a threatened population because marshlands in the Escambia County and Santa Rosa County area are particularly vulnerable to disturbance and alteration (Stevenson et al. 1978). Indeed, a potential threat to the East Bay population is the exploratory drilling for gas and oil that is about to get under way by Getty Oil Company in the Bay.

The Smyrna Seaside (*A. m. pelonota*) does not appear on the Game and Fresh Water Fish Commission list because at the time this list was prepared *pelonota* was considered by FCREPA (whose list formed the basis of the Commission's list) as Status Unknown (Baker and Kale 1978). MacGillivray's Seaside (*A. m. macgillivrayi*) is understandably not on the Florida list because it was not supposed to occur south of the Georgia line. This population should now be added to the Florida list in the Species of Special Concern category.

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Habitat Partitioning by Seaside and Song Sparrows

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Abstract. We compare Seaside Sparrow (*Ammospiza maritima maritima*) and Song Sparrow (*Melospiza melodia atlantica*) populations nesting on a small island in Chesapeake Bay in terms of the use of space and the vegetational factors that appear to influence spacial patterns. The two species showed a significant difference in habitat use for most activities. Our results suggest that the spatial distribution of the two sparrow populations is related to characteristics of the vegetation and shoreline.

Interspecific competition between two related species is often reduced by morphological and behavioral adaptations. Studies of the niche relationships among related sympatric species of birds and attempts to reveal ecological differences between sibling species have shown that they usually occupy different parts of the habitat and/or have different foraging and breeding habitats, which could facilitate stable coexistence (Lack 1944, 1954; Murray 1969). Patterns of habitat occupancy have been used to determine the competitive relationship and niche overlap among species. Differences in habitat selection could be based on a visual discrimination of vegetation types or characters such as leaf size and shape or light intensity (Gauthreaux 1972).

The Seaside Sparrow (*Ammospiza maritima maritima*) and Song Sparrow (*Melospiza melodia atlantica*) are breeding birds on South Island, Virginia. These species were compared in terms of the use of space and vegetation factors that appear to influence spatial patterns. The objective of this study was to determine what differences in the ecology of Seaside and Song Sparrows enable them to coexist in a relatively simple island environment.

STUDY AREA

South Island is part of a 2.4-km chain containing 100 ha of salt-marsh islands known as the Great Fox Island group, which is located in Chesapeake Bay (Fig.

1). It is slightly below the Maryland-Virginia line at 37°54'N by 75°54'W. South Island (Fig. 2), 3.4 ha in area, contains a high-salinity salt marsh dominated by Salt-marsh, or Smooth, Cordgrass (*Spartina alterniflora*) along the edge of the island and in the central area of tidal creeks and pools. Salt-meadow Cordgrass (*S. patens*) dominates the dry, higher elevations. Marsh Elder (*Iva frutescens*) forms a dense hedge on the western shore of the island. A sand dune plant community also occurs along the western shore. Panicum (*Panicum virgatum*), American Beach Grass (*Ammophila breviligulata*), and Seaside Goldenrod (*Solidago sempervirens*) are the dominant plants and appear to have stabilized the dune ridge (Fig. 2).

MATERIALS AND METHODS

Measurements of vegetation variables were made during the summers of 1977 and 1978. These variables objectively describe habitat characteristics that may be used as indicators or cues in habitat use by Seaside and Song Sparrows.

A 25-m × 50-m grid was established on the island to map vegetation and bird locations. Points of intersection of the grid lines were located using a meter tape and compass. Each point was marked with a wooden stake (5 cm × 5 cm × 2.8 m)

Vegetation Analysis

Random samples of 1 m² were taken in each grid block. The number and size of sample plots were determined by the homogeneity of the plant community

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and by use of a species-area curve. For each of the 90 sample plots, the plant species and percent of cover by individual species were visually estimated and recorded. The vegetation within each grid block was mapped, and a composite vegetation map of the island was constructed.

Observation of Sparrow Activity

Seaside and Song Sparrows were trapped using mist nets, and each was marked with a standard U.S. Fish and Wildlife Service band and a unique combination of colored plastic bands (red, white, and yellow). Birds were released at the site of capture. Fifteen sparrows were banded, accounting for all but two of the adult sparrows on South Island.

During a 3-month period from mid-May to mid-August, observations were made by walking through the study area and watching from a portable elevated platform. Sparrows were observed with binoculars. The individual bird's identity, activity, and elapsed time of activity as measured with a stop watch were recorded using the grid markers as points of reference. Vegetation, date, and time of day were also noted. The total activity space for each individual was determined by plotting all positions where it was seen. After activity spaces were mapped, the area of each was determined by using an area grid.

We examined data for all sparrows in terms of percent of total observation time and frequency of observations. Means and standard deviations were calculated for all categories of habitat use during the breeding season from the daily time budgets of individual birds. The student's *t*-test was used to determine differences in habitat use with a variable of 0.05 accepted as significant in all statistical tests.

RESULTS

Vegetation Analysis

The vegetation composition of the island, based on the dominant plant species, is shown in Figure 2, and percent of cover by major plant communities is shown in Table 1.

Observations of Sparrow Activity

A total of 1,240 observations (between 10 seconds and 30 minutes in duration) were made during the breeding season. Time budgets and the frequency of

observations were examined to determine patterns of habitat use.

Use of Space

On South Island, Seaside and Song Sparrows had all-purpose territories used for mating, nesting, loafing, displaying, and foraging. All territories were located in part of the perimeter of the island. Some spatial overlap of Seaside and Song Sparrow territories occurred in areas that furnished elevated perches, but usually, both species maintained mutually exclusive territories with few interspecific encounters. The vegetation composition of the Seaside and Song Sparrow territories is compared with that of the entire island in Table 1. Seaside Sparrow territories ranged from 3,445 m² to 4,533 m² with an average of 4,006 m². The Song Sparrow territories ranged from 1,454 m² to 3,757 m² with an average of 2,680 m². Territory size was based on observation of the male of each mated pair of sparrows.

DISCUSSION AND CONCLUSIONS

For Seaside and Song Sparrows on South Island, the distribution of the vegetation and location of the shoreline appear to be important in determining the spacing pattern of the two populations. Differences in habitat use are seen when the territories and activities of the two species are compared.

Marsh Elder, which covered 13.7% of the island, made up 45% of Song Sparrow territories but only 19.3% of Seaside Sparrow Territories. Marsh Elder and Panicum provided most of the elevated perches and may affect the pattern of habitat occupancy by the two sparrow species. Both Seaside and Song Sparrows used these elevated perches, but the tallest vegetation was dominated by the Song Sparrow. Seaside Sparrows used flight songs and perched on grasses and Black Needlerush (*Juncus roemerianus*) during territorial behavior. Vegetation height may be a less critical factor in habitat selection by this species.

The foraging habitats used by each of the two species were more distinctly separated. The Song Sparrow foraged primarily in the high-tide litter of the sand beaches. This made up 4.0% of the entire island but accounted for 14.2% of all Song Sparrow territories. Seaside Sparrows foraged in the cordgrass plant community and coarse wrack, which covered 45.0% of South Island and 62.0% of all Seaside Sparrow territories.

TABLE 1. Composition of Seaside and Song Sparrow territories on South Island, Chesapeake Bay, Virginia.

Plant community	Percent of island	Song Sparrow territories Percent of total (n = 3)	Mean percent	Seaside Sparrow territories Percent of total (n = 4)	Mean percent
Marsh Elder*	13.7	45.0	41.4	19.3	20.6
Salt-marsh Cordgrass*	45.0	3.9	4.8	62.0	59.9
Salt-meadow Cordgrass	23.0	14.4	15.8	14.3	14.9
Sand dune*	11.7	21.1	21.6	1.4	1.9
Sand beach*	4.0	14.2	15.0	0.5	0.4
Black Needlerush	0.9	0.9	1.3	1.7	1.8
Panne	0.2	-	-	-	-
Pools	1.4	-	-	0.7	0.9

*Significant difference in mean composition of territories between species.

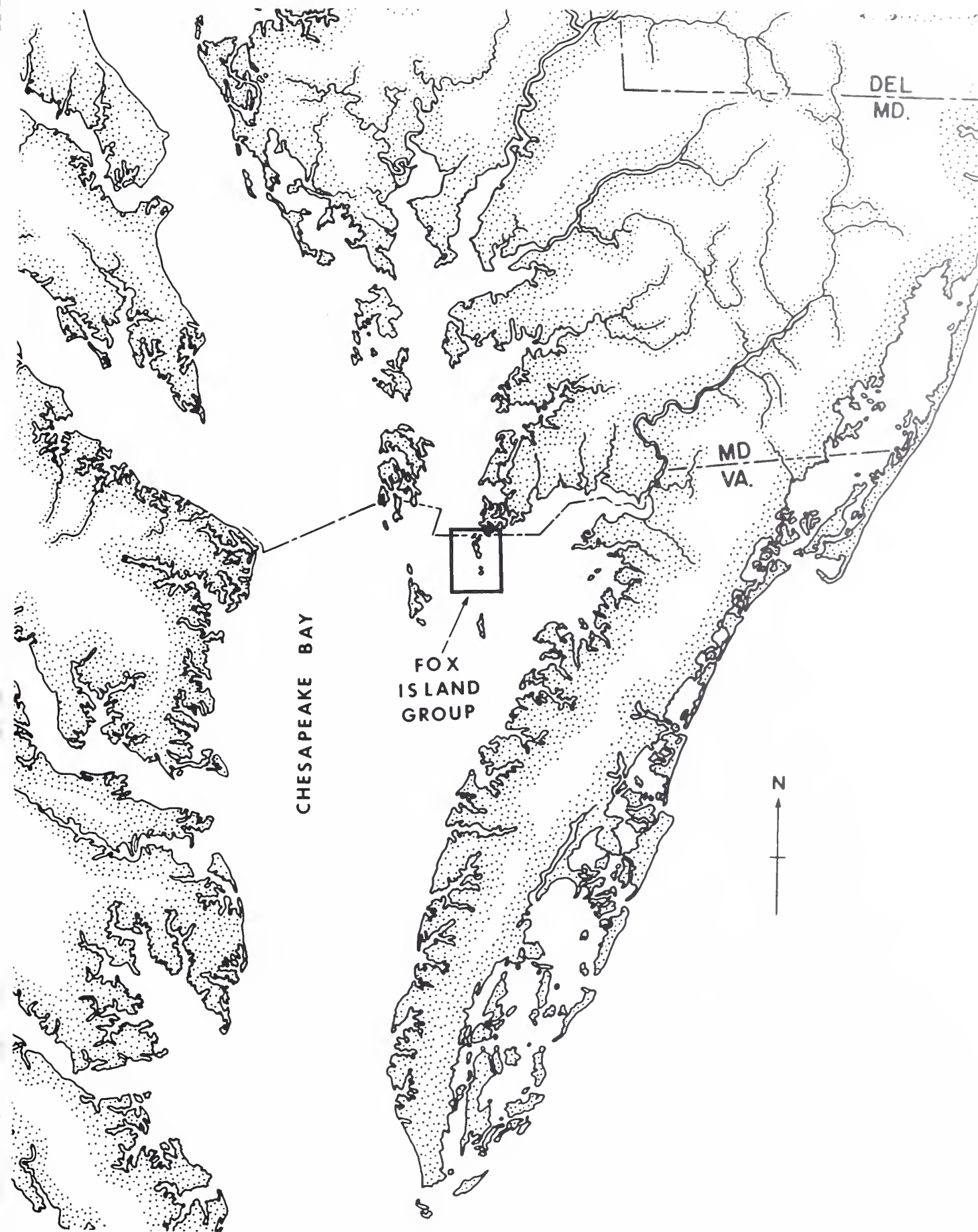


Fig. 1. General location of the Fox Island chain.

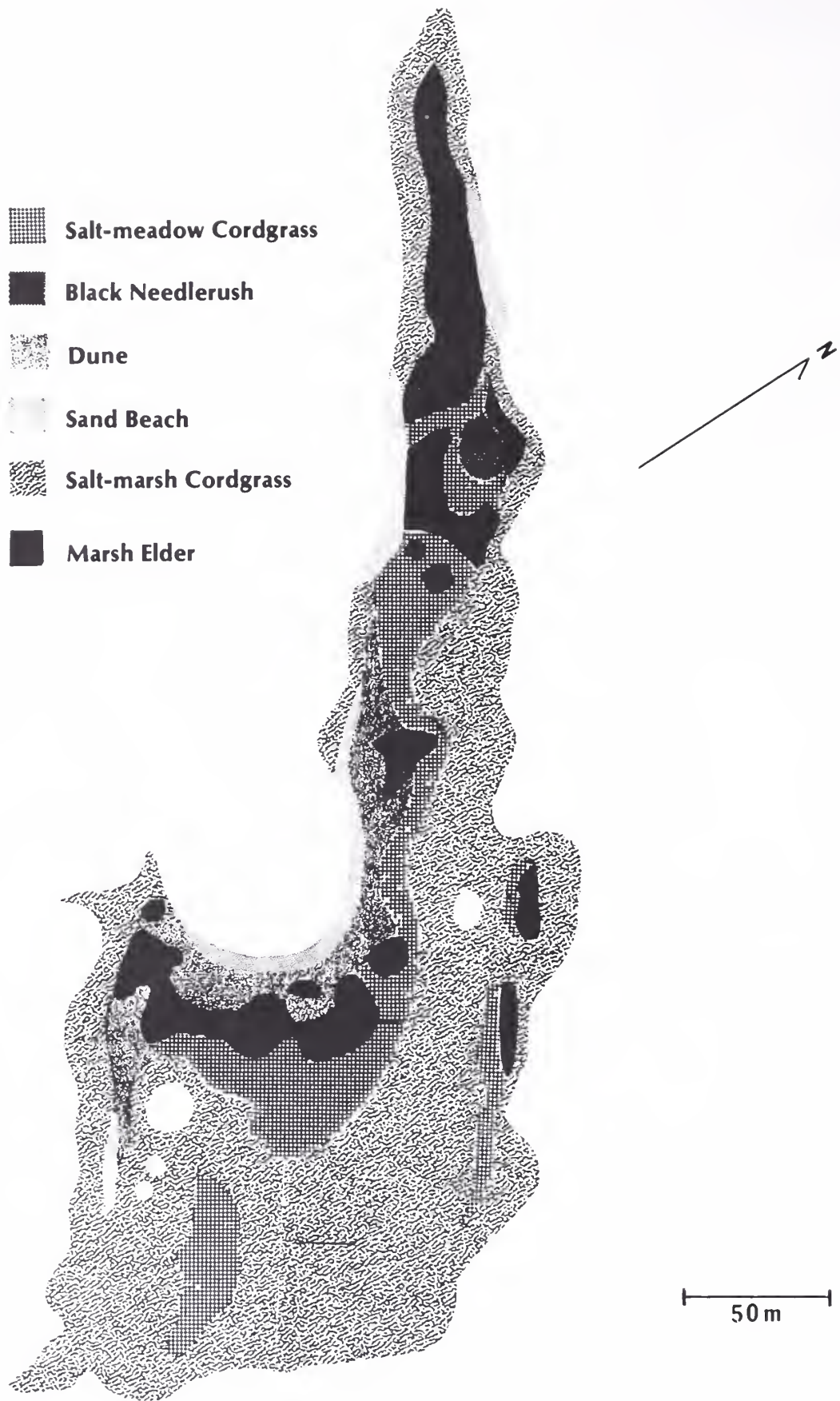


Fig. 2. Vegetation composition of South Island.

The nesting sites of the two species were in different habitats. Seaside Sparrows built in the cordgrass and rush communities. Song Sparrows built in areas of Marsh Elder.

Additional observations of Seaside and Song Sparrow populations were made on all other islands of the Great Fox chain, and differences in habitat selection were similar to those found on South Island.

Interspecific territoriality has been reported among similar species in simple homogeneous habitats such as marshes and grassland (Orians and Willson 1964). However, we believe that Seaside Sparrows and Song Sparrows on South Island are ecologically different enough to coexist without resorting to energy-expensive territorial behavior. The needs of both species with respect to feeding, nesting, and display apparently result in differences in habitat selection. Similarly, Cody (1968) found that grassland birds sharing an area exploit grassland conditions in different ways, thus permitting stable coexistence.

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The Cape Sable Sparrow: Its Habitat, Habits, and History

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Abstract. Potential habitat was surveyed by foot, boat, and helicopter to determine the distribution and habitat of the Cape Sable Sparrow (*Ammospiza maritima mirabilis*). From 1970 to 1975, the sparrows were found on Cape Sable, by Big Cypress Swamp, and adjacent to Taylor and Shark Sloughs. They inhabited clumped *Spartina* prairie, unclumped *Spartina* prairie, sparse *Cladium* prairie, and *Muhlenbergia* prairie. Most of the estimated 1,900 to 2,800 sparrows inhabited the *Muhlenbergia* prairies around Taylor Slough. This race avoids brushy prairie. Fire can be either beneficial, helping perpetuate and improve the habitat, or harmful, restricting nesting opportunities and destroying some birds. Highest sparrow densities in *Muhlenbergia* prairies were observed about 3 years after a fire; populations declined as the vegetation became decadent. Some habitat is threatened by exotic trees invading the prairie.

Some sparrows were marked with colored leg bands to study their habits, particularly their breeding biology. Males sang most in the early morning and in late afternoon and early evening. They defended 0.3- to 6.8-ha territories for mating, nesting, and feeding. Often pairs remained mated for successive nesting cycles. Normally three to four eggs were laid in either a domed or a cupped nest. Some females were triple-brooded, and successive broods fledged at 31- to 48-day intervals. The postbreeding emigrations of fledglings appear to be the principal mechanism of dispersal.

We suggest that differentiation of Seaside Sparrow races started during the Wisconsin glacial maximum in marshy deltas separated by high-energy coastline. As the sea level rose, marshes and Seaside Sparrows expanded. Final isolation of the Cape Sable Sparrow progenitors occurred as the rising sea and warming climate caused mangroves to displace the coastal marshes, forcing the sparrows inland to interior prairies.

The range of the Seaside Sparrow, *Ammospiza maritima*, extends through 15 degrees of latitude from Massachusetts to Texas. However, the species is restricted to coastal marshes, and its range is nowhere more than a few kilometers wide. Furthermore, acceptable habitat often is intersected by unacceptable habitats, dividing the sparrows' range into disjunct segments.

The most isolated of all Seaside Sparrow populations is the one restricted to the southern tip of Florida. This population was discovered by Arthur H. Howell on the coastal marl prairie on Cape Sable, Monroe County, Florida, in 1918. Described as *Thryospiza mirabilis*

(Howell 1919), the Cape Sable Sparrow recently was designated as a subspecies, *Ammospiza maritima mirabilis*, of the Seaside Sparrow (Eisenmann 1973). This race appears to have the most divergent habitat preferences of the nine recognized races. During the first 50 years following its discovery, little was learned about the biology of the Cape Sable Sparrow. Most publications (e.g. Howell 1919, Semple 1936, Dietrich 1938, Nicholson 1938, Anderson 1942, Stimson 1944, 1948, 1956) discussed primarily range extensions and population extirpations and rediscoveries. Exceptions include Nicholson (1928), Howell (1932), and Stimson (1954, 1968), who provide some information on natural history. The limited distribution and apparent extirpation of some populations of the Cape Sable Sparrow no doubt contributed to its classification as endangered by the

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U.S. Fish and Wildlife Service. This status, in part at least, provided the impetus for this research, which we began in 1969. Werner's field work gave special emphasis to defining the bird's habitat and also to obtaining life-history information, primarily through observing marked individuals during breeding. The information obtained on habitats and habits led to our speculations on the history of the race.

METHODS

Distribution and habitat were studied primarily in 1970, 1974, and 1975. Potentially occupied sites were located by consulting the literature, aerial photographs, and local naturalists (e.g. Louis Stimson) who were experienced with the race. The discovery of Cape Sable Sparrows in Taylor Slough (Ogden 1972) also prompted searching for the sparrows in some non-traditional habitats (e.g. *Muhlenbergia* prairies). As experience increased, aerial photographs (1:28000 black-and-white and 1:134000 color infra-red) became the principal tool for locating potential sites; sometimes these were supplemented by an aerial reconnaissance flight.

In 1970, surveys were conducted primarily on foot and by boat within the major coastal prairies landward of the mangrove swamps and glades between Collier-Seminole State Park and lower Shark Slough.

In 1974 and 1975, a helicopter was used extensively to survey all potential sites south of Okaloacoochee Slough and Alligator Alley. By repeatedly landing the helicopter, typically 7 to 16 sites were surveyed per morning and another 4 to 12 sites per evening. Surveys generally extended from daybreak to 1000 and from 1500 to dark. Furthermore, the helicopter provided an aerial platform from which one could view the habitat and improve at selecting sites from aerial photographs. Frequently sparrows were located before the helicopter blades stopped rotating. One morning of spot surveying by helicopter equaled about a week of survey on foot. Sharpe's (1968) technique of locating *A. m. nigrescens* from a moving helicopter was ineffective for locating Cape Sable Sparrows.

Concurrent with population surveys, the vegetation was described in each of the major habitats for both physiognomic and floristic structure. Species occurrence was described by frequency in square-meter quadrats and by plotless sampling using the "closest individual method" (Cottam and Curtis 1956). Physiognomic descriptions basically followed Wiens (1969). Binomial names of plants are from Avery and Loope (1980) and Black and Black (1980).

The climatological data (U.S. Dept. Commerce 1949-1975) were recorded at or near Taylor Slough. Air temperature was recorded at the Homestead Experiment Station; rainfall was recorded at the Royal Palm Ranger Station; and evaporation and wind were recorded at the Tamiami Ranger Station. These were the closest stations to the Taylor Slough study site having adequate historic records of the desired data.

Data on fire history were taken from maps and other records at Everglades National Park.

Most of the work on the sparrows' life history was accomplished near Ochopee, Monroe County, in 1970, and especially on the east side of Taylor Slough near

Pine Island, Dade County, in 1974 through 1976. The 150-ha Taylor Slough study site was marked with a grid of orange-flagged wire stakes at 91.44-m intervals. The 154-ha Ochopee study site was mapped on aerial photographs from ground surveys. It contained enough natural features for reference points to make a marked grid unnecessary.

The sparrows were marked with colored acetate leg bands (size B6) in combination with numbered U.S. Fish and Wildlife Service aluminum bands (size 1B), by placing the aluminum band on one leg and two colored acetate bands on the other leg. Nine colors of acetate bands were used. Acetate bands were not used on the same leg as the aluminum band because of slight differences in size. The total weight of one aluminum band and two acetate bands was 0.18 gm, about 0.9% of the birds' weight. The same technique was used on males, females, fledglings, and nestlings over 5 days old.

Most observations of adults and fledglings were made during morning and evening surveys. Territories were recorded by observing and recording the various locations of marked individuals on field maps. A blind was used some, but it proved impractical and soon was abandoned. Except during certain phases of their nest cycle, the sparrows appeared to ignore observers.

Individuals were sexed by inspection of the cloaca, then measured. Linear measurements were taken with calipers, and weights were measured using Pesola spring balances. The condition of molt and the presence of a brood patch were recorded. Where nests were located, nests, eggs, and nestlings were measured. Changes in nestling external morphology were recorded daily.

In 1974, duration and frequency of singing were recorded from a fixed point each Friday from 1 March through the middle of July. Song counts continued through the morning until less than five songs were recorded for a 15-minute time interval. Evening counts started before the late afternoon increase in singing started and continued until singing had completely stopped. In all, 62.5 hours were spent counting songs. All Cape Sable Sparrow songs were counted; however, most songs heard came from one individual that had a territory near the listening station. Later in the season, temperature also was recorded at 15-minute intervals with an unshaded thermometer.

Vocal and visual displays were described using terms from Post and Greenlaw (1975) where their published accounts indicated similarity. Otherwise, terms were assigned on the basis of phonetic characteristics. Several vocalizations were examined from audiospectrograms, prepared on a Kay Elemetric Sonagraph using the wide-band filter. The audiospectrograms were made at the Florida State Museum, using tapes from their Bioacoustics Archive recorded at Taylor Slough 16 and 17 April 1975.

HABITATS

Climate

South Florida usually is classified as subtropical by biogeographers. From January 1965 through January 1975 the monthly mean maximum air temperature at Taylor Slough ranged from a high of 32°C during August to a low of 25°C in February, a difference of

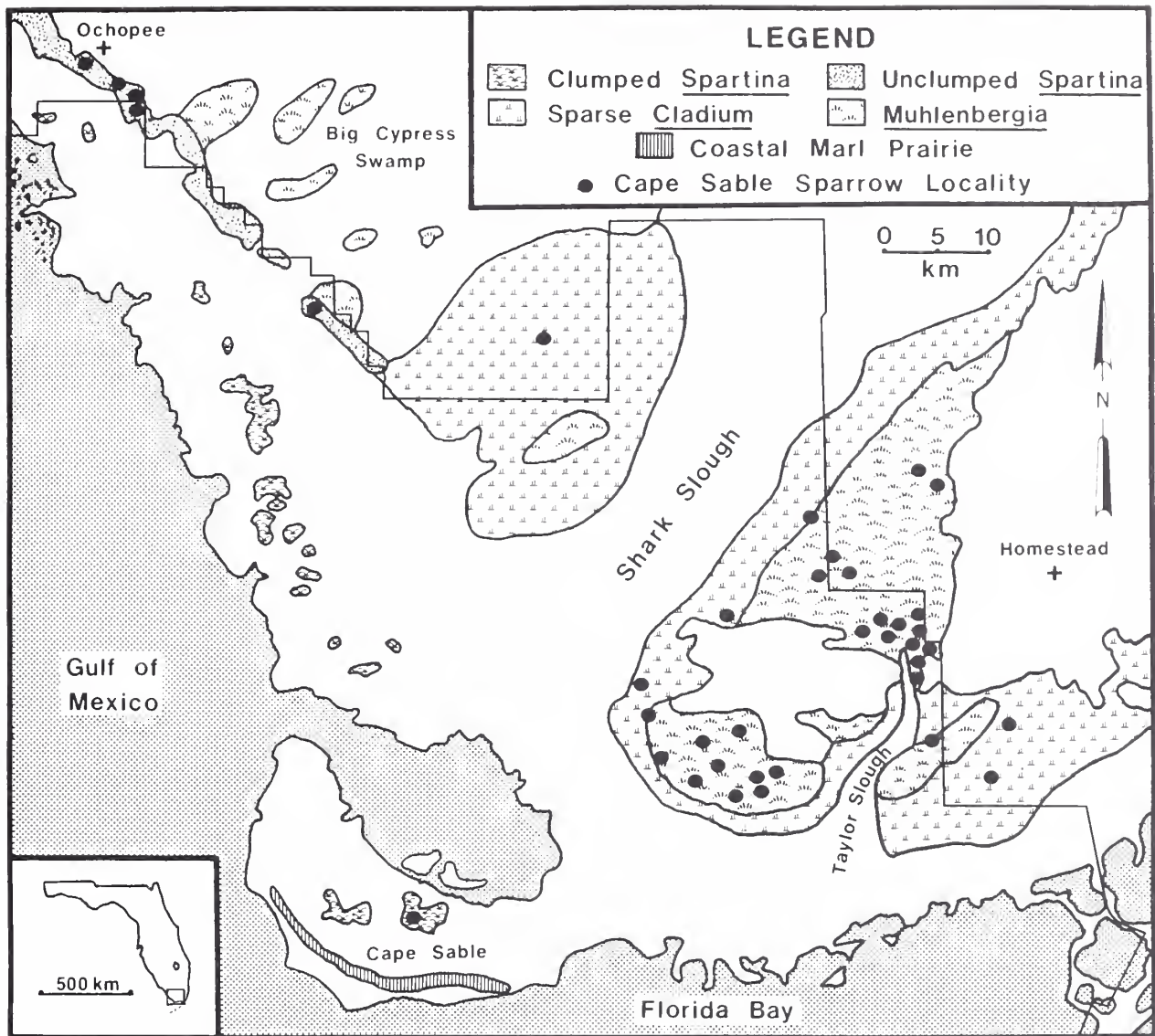


Fig. 1. Habitat and distribution of Cape Sable Sparrows, 1970-1975. Solid line delineates Everglades National Park boundary.

only 7°C. Monthly mean minimum temperatures show a slightly greater range of 10°C, from 22°C in August to 12°C in February. The difference between the mean annual maximum, 29°C, and mean annual minimum, 18°C, is 11°C. The mean difference between daily temperature extremes is slightly greater than the annual difference between mean monthly extremes.

South Florida has distinct wet and dry seasons. Most rain falls in the summer. December has the least rain; however, because of evaporation, the greatest water deficit occurs in March and April. Thus the dry season is a winter-spring phenomenon, which extends through the first half of the breeding season. Data for water gain via dew or loss through transpiration are not available; but during the dry season, the heavy early-morning dew may be an important source of moisture, providing water for the birds and moisture for the soil by "stem run-down" facilitated by smooth, involute leaves. This appears to be the major source of moisture during the dry season. Thus moisture may be important in moderating the microclimate within the vegetation,

where adult sparrows generally remain during the hottest part of the day. We conclude that Cape Sable Sparrows live in a climate similar to the tropical wet-and-dry climate described by Trewartha et al. (1967).

Vegetation

From 1970 through 1975, Cape Sable Sparrows were found in isolated populations on Cape Sable, near Big Cypress Swamp, and adjacent to Taylor and Shark Sloughs (Werner 1971, 1975, 1976, 1978; National Fish and Wildlife Laboratory 1980). They lived in four distinct habitats: clumped *Spartina* prairies, unclumped *Spartina* prairies, sparse *Cladium* prairies, and *Muhlenbergia* prairies (Fig. 1). A characterization of these habitats and floristic and physiognomic descriptions are presented in Figure 2 and Tables 1 and 2.

Clumped *Spartina* prairie: The clumped *Spartina* prairies are dominated by tall, generally clumped *Spartina bakeri*, a grass with a mean height of approximately 2 m. The *Spartina* cover is broken into a discontinuous pattern over most of the colony by creeks,

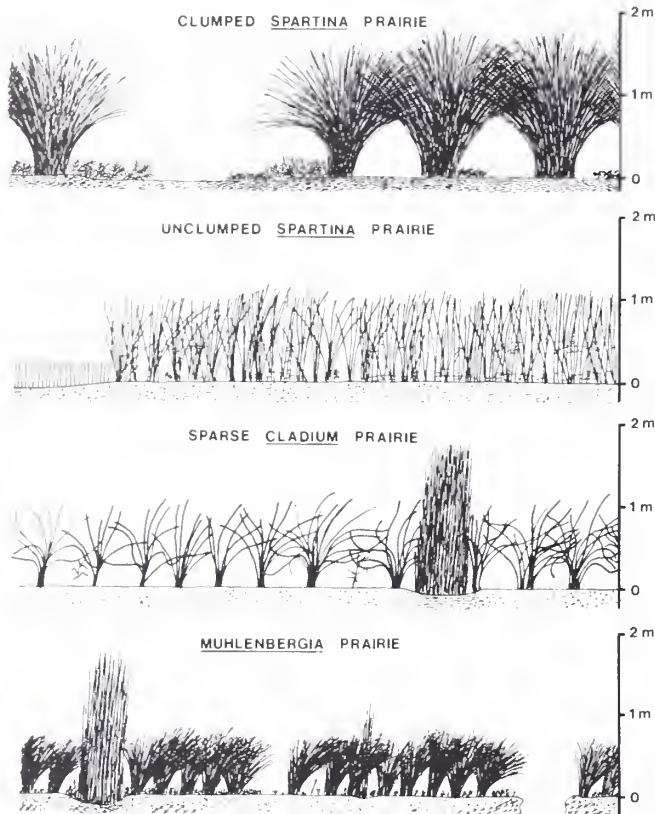


Fig. 2. Structural characterization of the four major habitats occupied by Cape Sable Sparrows.

ponds, and patches of shorter vegetation (*Distichlis spicata*, *Eleocharis cellulosa*, *Sesuvium* sp., and a few small *Laguncularia racemosa*). This interior prairie overlying loose organic soil is covered by shallow, slightly brackish water during most of the year. Some years this habitat appeared to be flooded continually.

The sparrows were found in this habitat only in the vicinity of East, Middle, and Little Fox Lakes on Cape Sable. The portion of the Fox Lake *Spartina* prairie not occupied by Cape Sable Sparrows lacks much of the heterogeneity of that occupied by the sparrow colonies. Homogeneous *Spartina* prairie forms dense, generally monospecific mats of tall grass broken only by scattered creeks, small ponds, and occasionally by invading *Laguncularia racemosa*. Similar *Spartina* prairies are scattered throughout the mangroves northward to Collier-Seminole State Park. Cape Sable Sparrows were not found in any of them, though they contained other vertebrates that occur sympatrically with the sparrows on the Fox Lake prairie.

Clumped *Spartina* prairies support few sparrows. In 1970 a minimum of four singing males and five fledglings were counted (Werner 1971). During the next 5 years only a few to none were found there. During the 6 years, 1970-1975, the Fox Lake prairie may have become more saline. Much of the *Eleocharis*, a freshwater sedge that had been common in 1970, was replaced by *Distichlis*, a grass of more saline environments. Patches of *Sesuvium*, a halophytic forb, appeared to have expanded also.

Formerly, *Spartina* prairies were more extensive on Cape Sable. Photographs taken along the Homestead Canal west of Gator Lake in 1924 show vast prairies of

Spartina bakeri dotted with occasional palm hammocks (Holt and Sutton 1926). Today this area is primarily mangroves, mud flats, and halophytic forbs.

Unclumped *Spartina* prairie: The unclumped *Spartina* prairie also is dominated by *Spartina bakeri*, but here it grows low (about 1 m) with an irregular distribution, instead of tall and clumped. In some places, where the habitat has not burned for several years, the *Spartina* has fallen over, forming dense mats pierced by new upright growth. The shallow soil (approximately 0.5 m deep) varies from gray to brown and is composed of marl, detritus, and quartz sand. The prairie is generally flooded except during the spring dry season.

This habitat is most common as a long, narrow band between Big Cypress Swamp and the mangrove swamps. The prairie is dissected by stands of *Eleocharis cellulosa*, Cat-tails (*Typha* sp.), Pond Cypress (*Taxodium ascendens*), and Bald Cypress (*T. distichum*). The *Spartina* prairie is dotted with small Cabbage Palm (*Sabal palmetto*) hammocks, and scattered patches of *Distichlis spicata* and *Juncus roemerianus*. Adjacent to Big Cypress Swamp the species diversity increased in the unclumped *Spartina* prairie as the grass mixed with *Cladium jamaicense*, *Panicum virgatum*, and other graminoids.

During the surveys, small (≤ 10 males) isolated colonies (annual total ≤ 27 sparrows/year) of the sparrow were found in this habitat where the *Spartina* was dissected by *Eleocharis*, dense matted *Spartina*, *Spartina* heavily integrated with *Cladium*, sparse *Typha* integrated with matted *Spartina*, and in mixed *Spartina*, *Cladium*, *Eleocharis*, and *Typha*.

Between 1970 and 1975 vast changes occurred in much of the Ochopee-Turner River region. At Ochopee much of the *Spartina* was replaced by *Juncus*, and the *Eleocharis* was replaced almost entirely by *Distichlis*. A large patch of *Typha* in the center of the site had almost disappeared. Near the Turner River vast stands of *Typha* have been replaced by *Spartina*. The region appears to have become more saline during these years.

Portions of the coastal marl prairies where the Cape Sable Sparrow was discovered may once have been unclumped *Spartina* prairie. The area was described as having Switchgrass or Cordgrass, both of which are common names for *Spartina*, in association with Salt Grass, *Distichlis*, and Sea Purslane, *Sesuvium* (Nicholson 1928, Semple 1936, Stimson 1954). A photograph taken in 1921 by G. R. Wilson of a typical nest site (Stimson 1968, plate 47) shows the habitat as primarily short sparse *Spartina bakeri* in association with *Distichlis*, which typifies some unclumped *Spartina* prairies.

Stimson (1968) postulated that the 1935 hurricane eliminated Cape Sable Sparrows from the coastal marl prairie. He further suggested that the birds seen later by Semple (1936) represented a subspecies of *Ammodramus maritima* other than *mirabilis*. Other races do occur on the coastal marl prairie in low numbers during the winter, primarily in flooded *Batis*. Semple (1936) reported seeing Cape Sable Sparrows in Switchgrass (*Spartina*) during the spring. The 1935 hurricane was not the only historically recent severe storm on Cape Sable. Between 1871 and 1973 eight hurricanes passed directly over the Cape, and some were of intensities

TABLE 1. Floristic description of dominant vegetation in the four major habitats occupied by Cape Sable Sparrows.

Habitat:	<i>Muhlenbergia</i>	Sparse <i>Cladium</i>	Unclumped <i>Spartina</i>	Clumped <i>Spartina</i>
Family and species	Frequency of dominance within square-meter quadrats per habitat*			
Poaceae				
<i>Muhlenbergia filipes</i>	88%	0%	0%	0%
<i>Panicum virgatum</i>	0%	0%	7%	0%
<i>Spartina bakeri</i>	0%	0%	53%	60%
Cyperaceae				
<i>Cladium jamaicense</i>	12%	100%	27%	0%
<i>Eleocharis cellulosa</i>	0%	0%	13%	15%
Aizoaceae				
<i>Sesuvium</i> sp.	0%	0%	0%	25%
	Relative density per habitat**			
Poaceae				
<i>Aristida</i> sp.	6%	0%	0%	0%
<i>Eragrostis elliottii</i>	2%	0%	0%	0%
<i>Muhlenbergia filipes</i>	40%	0%	0%	0%
<i>Panicum portoricense</i>	4%	0%	0%	0%
<i>Panicum tenerum</i>	0%	9%	0%	0%
<i>Schizachyrium rhizomatum</i>	2%	0%	0%	0%
<i>Spartina bakeri</i>	0%	0%	13%	40%
Cyperaceae				
<i>Cladium jamaicense</i>	12%	64%	27%	0%
<i>Eleocharis cellulosa</i>	0%	18%	27%	5%
<i>Rhynchospora microcarpa</i>	2%	0%	0%	0%
Juncaceae				
<i>Juncus roemerianus</i>	0%	0%	27%	0%
Aizoaceae				
<i>Sesuvium</i> sp.	0%	0%	6%	55%
Apiaceae				
<i>Centella asiatica</i>	8%	0%	0%	0%
Verbenaceae				
<i>Phyla nodiflora</i>	8%	0%	0%	0%
Scrophulariaceae				
<i>Bacopa caroliniana</i>	0%	9%	0%	0%
Asteraceae				
<i>Aster dumosus</i>	2%	0%	0%	0%
<i>Mikania scandens</i>	4%	0%	0%	0%
<i>Pluchea rosea</i>	8%	0%	0%	0%
<i>Solidago stricta</i>	2%	0%	0%	0%

* N = 50, 10, 15, 20 respectively

** N = 50, 11, 15, 20 respectively

similar to the 1935 storm (Gentry 1974). In Louisiana in 1957, *A. m. fisheri* was reported to have survived a severe hurricane that flooded local marshes with over 3 m of water (Newman 1957). Though Semple's observations are the most widely known, the sparrows also were reported after the hurricane by Dietrich (1938) and Sprunt (1938). Thomas Burleigh (1939) failed to find the sparrows in 1938, but he was searching for them in December when they are extremely secretive. Robert Woodmansee and Louis Stimson searched unsuccessfully for the sparrows on Cape Sable during the breeding season (Stimson 1956), but their search

was in 1949, 14 years after the hurricane. As discussed below, by then the habitat there may have become unsuitable. We suggest that the Cape Sable Sparrows that occupied the coastal marl prairie probably were not destroyed by the storm, but by rapid alteration of the habitat, which possibly was initiated or hastened by the 1935 storm. Today the vast stands of *Spartina* are gone; the coastal marl prairie has become a long narrow strip primarily of halophytic forbs (e.g. *Batis maritima*, *Sesuvium* sp., *Borrchia frutescens*). Large patches of *Distichlis* still are present, but are not associated extensively with *Spartina*. Both *Spartina bakeri* and

Spartina spartinae remain, but only as small, isolated patches; they too appear to have declined between 1970 and 1975.

Sparse *Cladium* prairie: The sparse *Cladium* prairie consists of short (about 1 m), sparse Sawgrass, *Cladium jamaicense*, growing on shallow (about 0.5 m) gray-marl soil, which is flooded much of the year, and includes widely spaced tree islands. Both floristically and structurally the region appears homogeneous. This habitat is widespread between Big Cypress Swamp and Shark Slough, on the periphery of Taylor and Shark Sloughs, and in extreme southeastern Florida.

In the early 1950s this habitat supported the most extensive known population of Cape Sable Sparrows, which extended from Gum Slough to Shark Slough. Though rare here from 1970 to 1975, more recent surveys again have found them widespread (Bass, pers. comm.). Possible reasons for fluctuations in the sparrow populations in this habitat are the effects of fire, which are discussed below in a separate section.

***Muhlenbergia* prairies:** *Muhlenbergia* prairies resemble sparse *Cladium* prairies in that they are vast, homogeneous expanses of short grass dotted with tree islands. Closer examination reveals generally clumped, short grass (about 0.7 m high) having involute, pointed leaves and growing on shallow gray-marl soil (about 0.2 m deep), which is flooded with fresh water for only a few months (mean = 80 days, range = 0-177 days, Taylor Slough study site, N = 14 years) during the summer and fall. *Muhlenbergia* prairie is dotted with small solution holes averaging about 1 to 4 m in diameter and about 0.25 to 0.5 m deep, which are filled with marl, organic soil, or both. Principal solution-hole plants include tall dense *Cladium*, forbs, and other graminoid vegetation typical of the deeper part of the slough (e.g. *Sagittaria lancifolia*, *Panicum hemitomon*); occasionally woody plants (especially *Salix caroliniana*) are present. In some areas the limestone bedrock, Miami Oolite, protrudes as pinnacle rock, and the vegetation is sparse. The sparrows avoid these rocky areas. Floristically, *Muhlenbergia* prairies are the most heterogeneous habitat used by Cape Sable Sparrows. Other plants common in this habitat include *Schizachyrium rhizomatum*, *Centella asiatica*, *Phyla nodiflora*, *Pluchea rosea*, *Rhynchospora microcarpa*, *Melanthera angustifolia*, and over 100 other species, principally forbs and graminoid vegetation. The sparrows seem to avoid those places where considerable brush has invaded the prairie. At Taylor Slough the maximum forb height was significantly greater ($P < 0.01$) in unoccupied prairie. The general resemblance of large forbs to woody plants (brush) further substantiates the apparent avoidance by Cape Sable Sparrows of brushy prairie. The major *Muhlenbergia* prairies extend from Everglades National Park's Hole-in-the-donut farmlands south toward the north edge of Craighead Basin and northeast from Long Pine Key to Grossman Hammock. Some *Muhlenbergia* grows north of Shark Slough below the E.N.P. boundary. Similar, but smaller, prairies are in the Long Pine Key "finger glades" and in various interior portions of Big Cypress Swamp, but the sparrows have not been found in either place.

Cape Sable Sparrows were first discovered in this habitat in 1972 (Ogden 1972). Although they were reported at Taylor Slough as early as 1957 (Mr. and Mrs. W. M. Klein, Everglades National Park records), the record was not corroborated. Surveys in 1974 and 1975 showed that *Muhlenbergia* prairie supported one of the largest and most viable populations of the sparrows known. The Taylor Slough population, which lives primarily in *Muhlenbergia* prairie, was estimated at 1,900 to 2,800 sparrows based on surveys in 1974 and 1975 (Werner 1976).

Muhlenbergia prairie, which currently appears to be the best habitat for the sparrows, may have been rare in the past. Some older South Florida naturalists (e.g. Craighead, pers. comm.) claim that the recent destruction by drought fires of the shallow organic soil, which formerly overlaid the marl (Craighead 1974), and the general drying of South Florida has propagated the vast *Muhlenbergia* prairies that exist today. John H. Davis Jr., who conducted extensive surveys of South Florida's natural features (Davis 1943) about 42 years ago, describes no *Muhlenbergia*-dominated prairie communities, nor does he discuss *Muhlenbergia* as a component of those prairies where at present it predominates. Davis describes these places as "marsh prairies" composed of "switch-grasses, poverty grasses, beak-rushes, needle-grass, black sedge, and sawgrass." Sawgrass once dominated the prairie south of the "Miami rockland pine forests" (Davis 1943). Today this prairie is predominantly *Muhlenbergia* except for *Cladium* near the mangroves and on most of the prairie east of Taylor Slough. This raises the question, "Did recent alterations in South Florida promote the large size of the Taylor Slough population, or was the current Taylor Slough population formerly as large as, or larger than, it is today?" Unfortunately we do not know how to answer this question.

The extent of the prairie at Taylor Slough, both *Muhlenbergia* and *Cladium*, is decreasing because of the spread of exotic trees (*Casuarina litorea*, *C. glauca*, *Melaleuca quinquenervia*, and *Schinus terebinthifolius*). Much of the prairie near Grossman Hammock and southeast of Homestead also once may have been acceptable habitat for Cape Sable Sparrows. However, in recent years these regions also have been invaded by exotics, principally *C. litorea*. *Schinus* and *Melaleuca* now are invading many portions of these same areas. The rate of spread of these exotics seems sufficiently rapid to change a prairie to forest within several years, which of course eliminates the sparrows. Eventually these exotics reduce the natural community almost to a monoculture (Alexander and Crook 1974), which has no resemblance to the structural or floristic components of the original system. Early writers reported Cape Sable Sparrows in *Spartina patens*, both at Big Cypress (Stimson 1956) and on Cape Sable (Howell 1932). *Spartina patens* was not found at either locality from 1970 to 1975.

Both *Distichlis spicata* and *Juncus roemerianus* grow in South Florida and are reported as habitat components for certain other races of Seaside Sparrows (Tomkins 1941, Austin 1968, Norris 1968, Sharpe 1968). Monocultures of *Juncus* are extensive within the mangrove swamps and at scattered locations in the prairie

TABLE 2. General physiognomic description of dominant vegetation in the four major habitats occupied by Cape Sable Sparrows.

FEATURE	Habitat: <i>Muhlenbergia</i>	Sparse <i>Cladium</i>	Unclumped <i>Spartina</i>	Clumped <i>Spartina</i>
Dispersion*	small distinct clumps	irregular or uneven	irregular or uneven	large distinct clumps
Biomass	100-1,100 gm/m ²	600-900 gm/m ²	500-3,100 gm/m ²	3,100-3,400 gm/m ²
Density**	1,300-2,400 ind./m ²	≈800 ind./m ²	≈1,100 ind./m ²	≈1,400 ind./m ²
Stand height	≈0.7 m	≈1 m	≈1 m	≈2 m
Stand color***	tan-green	light green	tan-light green	tan-light green
Stem angle*	75-90°	≈90°	75-90°	75-90°
Stem display	straight	straight	straight	straight
Stem thickness	1-2 mm	1-8 mm	1-5 mm	1-6 mm
Leaf shape*	very narrow	very narrow	very narrow	very narrow
Leaf size*	nanophyll-microphyll	mesophyll	mesophyll	mesophyll
Leaf display*	vertical	vertical	vertical	vertical
Leaf texture	smooth-pointed	smooth-serrate	smooth-scabrous	smooth-scabrous
Leaf type*	simple	simple	simple	simple
Leaf function*	evergreen	evergreen	evergreen	evergreen

* Terms in Wiens (1969).

** Calculated using "Closest Individual Method" (Cottam and Curtis 1956).

*** Color variation caused by season and age of stand since burned.

east of the mangroves. However, we know of only one record of the Cape Sable Sparrow in *Juncus* (Stimson 1954). In 1970, in the Ochopee-Turner River region where some sparrow colonies lived, *Juncus* was present in association with *Spartina bakeri*, but only as a minor component of the vegetation. Sweep samples suggest that South Florida *Juncus* harbors fewer macroinvertebrates than other South Florida prairies (E.N.P. fire files). In South Florida, *Juncus* grows inland rather than coastally where tidal invertebrates also would be available. Food may be a limiting factor for the sparrows in South Florida *Juncus* monocultures.

Distichlis is a minor habitat component of sparrow colonies both on Cape Sable and near Big Cypress Swamp. Nicholson (1928) reported nests in *Distichlis*. However, during this study Cape Sable Sparrows were not observed where *Distichlis* forms extensive monocultures. Perhaps the thick, matted growth provides insufficient cover and interferes with their ability to run over the ground. Norris (1968) noted that breeding populations of *A. m. fisheri* seem to need the clumps of *Juncus* scattered in the *Distichlis*. *Distichlis* marshes lacking the *Juncus* clumps seem to be used only by wintering individuals.

Several South Florida prairie communities appear not to be inhabited by Cape Sable Sparrows. Uninhabited communities include tall *Cladium jamaicense* prairies in the eastern portion of the mangrove swamps, coastal Spike-rush (*Eleocharis*) marshes adjacent to mangrove swamps, extensive *Typha* monocultures southwest of Big Cypress Swamp, and slough prairies,

which usually are a mosaic of tree islands, tall *C. jamaicense*, and short graminoid vegetation (e.g. *E. cellulosa*, *Rhynchospora tracyi*, *Panicum* sp.). These brackish to freshwater habitats generally have relatively long hydroperiods, and the graminoid vegetation is either taller and denser or shorter and sparser than in the habitats known to be occupied by Cape Sable Sparrows.

Sympatric Animals

The bird fauna that lives sympatrically with Cape Sable Sparrows is similar in all habitats occupied by the sparrow. The most common wintering birds and their estimated densities in the *Muhlenbergia* prairies of upper Taylor Slough are the Short-billed Marsh Wren, *Cistothorus platensis* (6-52/40 ha), Common Yellowthroat, *Geothlypis trichas* (5-10/40 ha), Eastern Meadowlark, *Sturnella magna* (6-7/40 ha), Red-winged Blackbird, *Agelaius phoeniceus* (1-2/40 ha), Savannah Sparrow, *Passerculus sandwichensis* (5-10/40 ha), and Swamp Sparrow, *Melospiza georgiana* (10-17/40 ha). Occasionally Marsh Hawks, *Circus cyaneus*, forage over the prairie. Few interspecific interactions were observed with wintering sympatrics. Once a Cape Sable Sparrow was seen foraging within several meters of a Swamp Sparrow. Another time, in March, which is at the beginning of its breeding season, a male Cape Sable Sparrow chased a Swamp Sparrow from its perch. Most of the wintering birds do not depart until after Cape Sable Sparrows have begun to breed in late February or early March. Short-billed Marsh Wrens have been seen in the Taylor Slough study site as late as 21

April, Swamp Sparrows as late as 30 April, and Savannah Sparrows as late as 5 May.

Eastern Meadowlarks, Common Yellowthroats, and Red-winged Blackbirds are resident in varying numbers throughout the year. Eastern Meadowlarks appear to occupy the most similar habitat, nesting and foraging in the prairies. Unlike the sparrows, however, they are tolerant of a much greater diversity of habitats and move into burned prairies earlier than do the sparrows. Breeding by Eastern Meadowlarks appears to begin in early February and to extend into early July. Winter and breeding densities are similar. Breeding yellowthroat populations seem no more than 1/40 ha on the *Muhlenbergia* prairie, where they probably nest in the Sawgrass and willows associated with some of the larger solution holes. They are common in the *Spartina* prairies and in the deeper parts of sloughs. During the breeding season, Red-winged Blackbirds appear to increase slightly to 2-3/40 ha on that portion of the *Muhlenbergia* prairie occupied by the sparrows; however, their breeding density is much greater on the high rocky portions of the prairie, which generally are not used by the sparrows, and where brush and tree islands are more frequent. On the prairie, Red-winged Blackbirds appear not to begin breeding until late March or April and seem to terminate in June or July. Red-winged Blackbirds interact aggressively toward the sparrows. Cape Sable Sparrows vacate exposed perches when approached by them, and several times Red-winged Blackbirds, usually females, actually chased male sparrows from their perch. Sometimes several Red-winged Blackbirds pursued one sparrow, which escaped—usually by darting, diving, or moving into the grass. Limited observations suggested to us that Red-winged Blackbirds also were the most serious avian competitor of the Dusky Seaside Sparrow.

The Common Nighthawk (*Chordeiles minor*) is common over *Muhlenbergia* prairies, arriving in April and departing about September. They nest on the lime-rock or marl in open areas, or on prairies at an early stage of succession after a fire. One nighthawk laid its eggs where a m² of vegetation had been removed. In *Muhlenbergia* prairie inhabited by the sparrows, nighthawk densities appear to be less than 1/40 ha, though many individuals are observed overhead; in the adjacent, more rocky prairie, the breeding density is greater. Nighthawk nesting on the prairies is possible only prior to summer flooding.

Boat-tailed Grackles (*Quiscalus major*) are common breeders in Taylor Slough, where they nest in the *Salix* and *Phragmites* but not on the *Muhlenbergia* prairie. Anuran choruses, which peak in May and June, during the latter part of the sparrow breeding season, often are so loud that singing male sparrows are barely audible to humans. The abundant participants are *Gastrophryne carolinensis*, *Bufo quercicus*, *Hyla squirella*, *Pseudacris nigrita*, and *Limnaeodius ocularis* (binomial names from Conant 1975). Whether or not the din affects the sparrows remains unknown.

Several sympatric animals are potential predators on Cape Sable Sparrows, but only two are known to feed on them. Once an adult sparrow was found in a Short-tailed Hawk (*Buteo brachyurus*) nest (Ogden 1972). Ants are known to kill nestlings. Twice, while nestlings were being measured, the young remaining in the nest

were attacked by ants in the absence of adults. The first time, upon the observer's prompt departure from the site, the parents returned, preventing any losses. The second time the problem was more severe, and one nestling was killed; the other three lived to fledge. Predation on adult sparrows appears low. During the year between the onset of their breeding in 1974 and 1975, only 2 of 16 males (12.5%) at one study area disappeared. During the 1975 breeding season, 2 of 28 resident males (7%) disappeared. Predation on adults might be heaviest during summer floods when much of their protective cover is submerged, making it difficult for the sparrows to evade enemies by running under the dense, short grass. Fledgling mortality was not estimated because of suspected dispersal from the immediate nesting area.

Fire

Though only an ephemeral component of the prairie, fire has a major influence on the composition and structure of Cape Sable Sparrow habitat. Fires either aid or harm sparrows, depending on frequency of burning, percent of contiguous habitat burned, pattern of the burn, size and percent of the colony evicted, and proximity of the colony to adjacent colonies.

About five decades have passed since fire was first recognized as a threat to Cape Sable Sparrows (Holt and Sutton 1926). Since then, the elimination of the sparrows by fire from various regions of Big Cypress Swamp has been reported (Stimson 1968). Decline of the sparrows between the mid 1950s and early 1970s was especially obvious within the extensive region between Gum Slough and Shark Slough, though recently they have recovered there (Bass, pers. comm.). During the early 1970s, fires in Big Cypress Swamp seemed more frequent than in other South Florida prairies. The fires often were large, sometimes burning as much as 25,800 ha (e.g. Binky Fire, Taylor 1981). Fuel accumulation is sufficient for the prairie to burn every other year.

Cape Sable Sparrows may or may not use a prairie the spring following a burn, depending, in part, on the adequacy of cover. Natural fires, caused by lightning, occur principally during the summer rainy season and overlap only the latter portion of the sparrow's breeding season. Fires during the dry season (November-May), which primarily are man-caused, tend to burn more acreage than lightning-caused fires (Taylor 1981) because of the drier conditions. Regardless of when in the year a fire occurs, it prevents breeding at that locality during the ensuing season. Observations at various sites after burning suggest that summer and early-winter fires, either natural or man-caused, may have fewer deleterious effects on the sparrows than late-winter and spring fires, the latter generally being man-caused. While essentially all fires eliminate the first breeding season after the fire, by the second breeding season after summer to early-winter fires, the composition and biomass of the habitat can support a moderately dense sparrow population. If burned during the late winter or spring, not only is that breeding season eliminated but also, sometimes, the one thereafter. If breeding does occur, the habitat may support only a sparse breeding population. The widespread decline of

Cape Sable Sparrows on the vast prairie of the southern portion of Big Cypress Swamp may have been caused by successive years of extensive fire primarily during the spring breeding season, which, in association with the sparrow's life span of an estimated 3 to 4 years, reduced natality well below the population's normal mortality.

As already stated, small isolated *Muhlenbergia* prairies within Big Cypress Swamp appear to be adequate habitat for the sparrows, but none were found there between 1970 and 1975. In that region, many of the prairies were dissected by broad sloughs or stands of cypress forest. When the entire prairie burned, no sparrow refuges existed nearby. A similar problem with small patches of isolated habitat appears to exist in prairies within mangrove swamps, though fires occur less frequently there. Assuming these prairies are habitable by the sparrows, successful colonization seems unlikely to exceed extirpation because of the barriers, the high frequency of fire, and the short life span of the bird.

Though eggs and nestlings are always vulnerable, man-caused fires with multiple ignition points and fires where spotting is common also may kill some adults and fledglings. In northern Taylor Slough several marked sparrows were observed during a prairie fire on 21 January 1974. One individual continued to move in advance of the fire, allowing the fire to approach within several meters before flushing. When forced to the edge of the slough, it crossed and flew into some Sawgrass. Another individual was observed between three spot fires. As the fires burned closer together, the bird was last seen flying in a circle as the smoke and flames joined and obscured the bird. The sparrow may have escaped by flying up and out through the smoke. Slightly over one year later, the site was populated with a sparrow density similar to the preburn condition. Although most of the sparrows had been marked prior to the fire, no marked ones were seen thereafter, not even in unburned areas.

Distribution surveys at Taylor Slough suggest that fire is not always harmful to the birds, as the sparrows occurred even on prairies burned several times by large drought fires during the breeding season. During dry conditions in February 1972, an area of about 6,200 ha burned; approximately the same area had burned previously in 1957. In 1974, two sites within the perimeter of the burned area were preselected as potential habitat as determined by vegetation characteristics revealed on aerial photographs. When surveyed, both sites contained sparrows. E.N.P. fire records show that more than 40 fires that extended over 100 ha burned in the general region of the Taylor Slough population during the last 25 years.

In upper Taylor Slough, Cape Sable Sparrow densities vary with the age of the vegetation (rough) after a fire. A rough burned shortly before the breeding season contained no sparrows; however, the following year the density was 11 males/40 ha. In progressively older roughs, male densities were estimated at 13 males/40 ha (2-year rough), 20 males/40 ha (3-yr rough), 4 males/40 ha (4-yr rough), 4 males/40 ha (5-yr rough) and no males/40 ha (6-yr rough). One male living in the 6-year rough moved to the adjacent 2-year rough; the

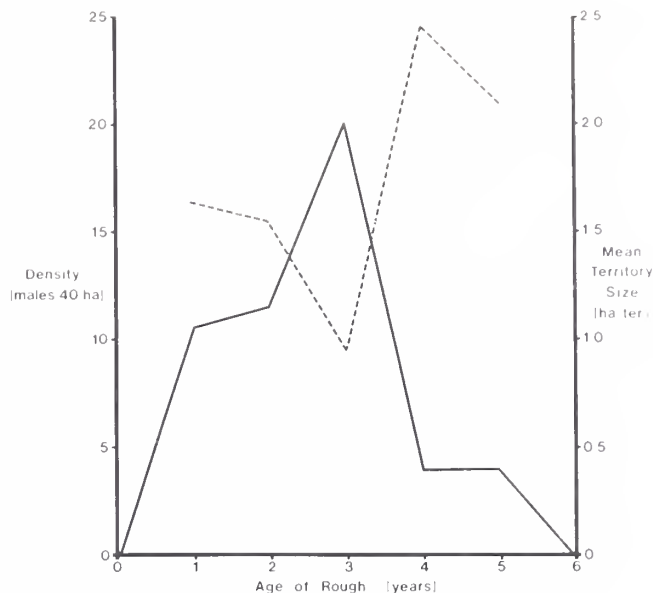


Fig. 3. Observed density (solid line) and mean territory size (dashed line) in various-aged roughs at Taylor Slough.

others disappeared. The sparrows are known to inhabit roughs over 5 years old; however, density is low. The area surveyed for the 4- and 5-year rough was not studied previously for density; but reports by others (Ogden 1972, pers. comm.) and Werner's observations suggest that densities in the 2- and 3-year rough were at least twice that of the same area 4 and 5 years after burning. Territory size showed an inverse relationship to density (Fig. 3). Vegetation samples indicated that the habitat attained its maximum biomass within 3 years after burning and that the ratio of dead to live biomass was greatest after that period (Werner 1976). The old, fragile, dead vegetation, which becomes a larger portion of the biomass after the third year, continues to be a major portion of the biomass even though the total biomass appears to fluctuate. Perhaps a slow rate of decay in the prolonged absence of fire leads to the accumulation of essential materials in the dead biomass as well as reduced growth through shading. We conclude that in *Muhlenbergia* prairie, decreased sparrow density and increased territory size may be related to decreasing ratios of live biomass and increasing amounts of old dead biomass after 3 years.

A similar relationship between sparrow density and vegetation age might exist in the other occupied habitats. Both *Spartina* and *Cladium* appear to collect dead biomass as the stand ages. However, the sparrow population in these habitats was too low for us to assess this relationship.

In the absence of burning, Cape Sable Sparrows also would be threatened by the natural succession of Everglades prairies to hardwoods. Fire retards hardwood invasion, perpetuating the prairie (Craighead 1971). Though man-caused wildfire may have been responsible for the species' widespread decline at Big Cypress Swamp, natural wildfires and carefully managed prescribed burns may be vitally important tools for sparrow management in the future. Certainly the role of fire in perpetuating the habitat is more important than any direct mortality it may cause (Robertson

and Kushlan 1974). Fire is an ancient component of the Everglades system (Cohen 1974). It seems unlikely that any population that evolved in a fire-maintained environment could be destroyed by that environment, unless the system was altered drastically by man.

HABITS

Vocalizations

The primary song of the Cape Sable Sparrow (Fig. 4) begins with a few weak clicks and terminates in a buzzy trill. The bird's head bobs up and down during the introductory clicks, then tilts slightly up and back as the song is completed. The primary song, which typically is delivered from a conspicuous perch, appears to function principally as a proclamation of territory. Most singing occurs during the breeding season, from February and March into July; however, at least a few songs were heard on certain days during every month of the year at Taylor Slough. Generally, two or more neighboring males sing alternately. When they do sing simultaneously, the routine is seldom repeated, and the songs often sound prematurely shortened. After a period of quite, singing by one male frequently appears to provoke singing by other males. When a person enters sparrow habitat during a quite period, such as during the middle of the day, occasionally a male sparrow will fly toward the human intruder, perch, and sing.

A song lasts about 1.5 seconds with 10 to 13 songs per minute given during bouts of persistent singing. Song counts (for all individuals heard) at Taylor Slough during the normal peak of singing (near sunrise) varied from 36 to 629 songs per hour (recorded on 12 April and 7 June 1974, respectively). This is an average of 0.6 to 10.5 songs per minute when measured over an extended time interval (1 hour), during which the singer takes breaks for preening, feeding, and so forth. Mean song frequencies of 10.6 songs per minute (Post and Greenlaw 1975) and 6.6 songs per minute (Woolfenden 1968) were reported for the northern race, *A. m. maritima*.

Cape Sable Sparrows sing most during the early morning and from late afternoon to early evening. Singing was heard as early as 56 minutes before sunrise and as late as 62 minutes after sunset. Generally singing began about one-half hour before sunrise and lasted 2 to 3 hours, sometimes 5 hours. Unmated males were the most persistent singers. On clear days, singing decreased shortly after the temperature rose to around 31-33°C (unshaded thermometer). There was little or no singing when the temperature exceeded 35°C in the sun. Singing seemed to last longer on overcast days, but apparently was little influenced by other normal weather phenomena such as early-morning fog. During the rare cool mornings following a cold front, singing usually was infrequent. Stage in the nest cycle clearly affects singing activity. At known nests, singing decreased abruptly once eggs hatched. Both paired and bachelor males occasionally sang during the middle of the day throughout the breeding season. The evening song period generally lasted from 0.5 to 2 hours and terminated about 0.5 hour after sunset. Singing during the nonbreeding season usually consisted of a few songs just prior to total darkness. During light rain showers, Cape Sable Sparrows persisted in their singing. Several

attempts to detect singing during heavy torrential thunderstorms failed, perhaps because of the noises of the wind, rain, and thunder. Sparrows did sing during the initial and terminal portions of these storms.

The song of the Cape Sable Sparrow is not loud, and even under optimal conditions could not be heard by Werner from more than about 200 m away. Stimson (1968) reported that he could hear the sparrows "a quarter mile" away. In Werner's experience, individuals that sounded very distant actually were very close, sometimes no more than 50 m distant.

The abbreviated primary song lacks the introductory notes and has an abbreviated terminal motif (Fig. 4). It is common for persistent singers to switch periodically, but briefly, from the primary song to the abbreviated primary song.

The whispering primary song is barely audible at the normal closest distance (ca. 20 m) to which an observer can approach a singer. The song resembles either the primary song or the abbreviated primary song but is given at a lower amplitude. When two singing males are within several meters of each other, one male generally will switch to the whispering primary song. On several occasions, singing males switched to whispering primary song when people approached them.

In July and August, fledglings sing subsongs that sound much like the primary song of adults. Gurgling sounds composed of various harsh notes also are heard from the fledglings. Their sound and pattern do not appear to relate to any known adult vocalizations. Both of these vocalizations can be heard in flocks of fledglings.

The *chip* call (Fig. 4), which appears to be a general-purpose communication, is common to male and female adults, fledglings, and nestlings. It is associated with territorial disputes, postbreeding flocking, nest defense, general alarm, and occasionally with complex flight vocalizations. On one occasion, chipping increased when a jet airplane flew low over the colony. *Chip* calls are often the most common vocalization during the nonbreeding season. This call was first heard from nestlings when they were 7 days old.

Occasionally, wing-tail flicking accompanies the *chip* call, especially when the bird is alarmed; sometimes wing-tail flicking is observed without the *chip* call. Though audiospectrograms indicate that the *chip* call most nearly matches the *tuck* call (Post and Greenlaw 1975) of the nominate race, Post and Greenlaw (1975) did not report wing-tail flicking associated with the *tuck* call.

The *tsip* call (Fig. 4) is high-pitched; it is used during a high level of anxiety, and usually is associated with nest defense or ground combat between males. Occasionally it is associated with complex flight vocalization. Both male and female adults can produce this call. The pattern of delivery resembles *chip* calls, consisting of irregular, but nearly continuous, repetition. Often the delivery appears more rapid than most *chip* calls. The accompanying visual display is tail jerking in which the tail is moved downward when the call is uttered. Though Woolfenden (1968) reported the same visual display for the nominate race, Post and Greenlaw (1975) reported wing-tail flicking.

Rapid, regular production of the *tsip* call produced a *si* twitter that was characteristically associated with

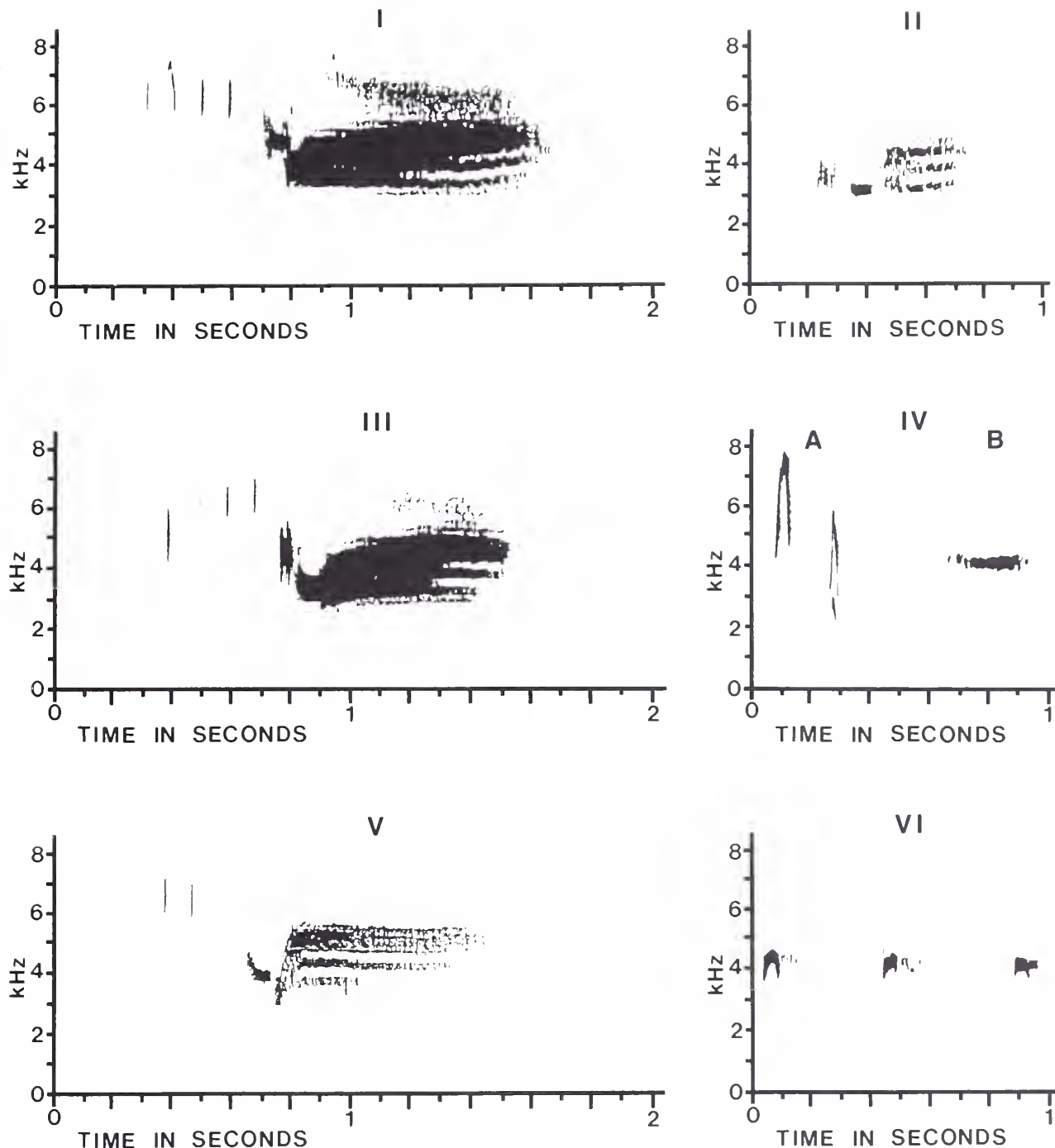


Fig. 4. Photoreductions of audiospectrograms of Cape Sable Sparrow vocalizations with background noise removed. I, III, and V—variations of the primary song. II—abbreviated primary song. IV A—variations of the *chip* call from separate audiospectrograms. Proximity does not reflect normal interval between utterances. IV B—*seeep* note. VI—*tsip* calls in actual sequence.

the initial portion of the complex flight vocalization and occasionally with chasing and combat. *Si* twittering is known only for male Cape Sable Sparrows.

Complex flight vocalizations occur sporadically throughout the year, but are most frequent during the early part of the breeding season (March-May). During a typical complex flight vocalization, a male ascends at a 30 to 40° angle to an estimated 5 to 15 m, making *si* twittering and sometimes *tsip* and *chip* calls on the ascent. Beginning at the peak of the ascent, the male sings the abbreviated primary song while descending

nearly vertically. This is usually followed by a short, quiet flight over the grass into which the male drops from sight. Occasionally the male sings twice while in the air by checking his descent and flying forward while giving the second and more abrupt abbreviated song. The double rendition was noted for 27% of the flight songs (N = 96) at Taylor Slough. In the Big Cypress and Cape Sable populations, only the normal flight song was heard (N = 7). Complex flight vocalizations occur throughout the day, possibly with greater frequency during the morning and evening. Sometimes an indi-

TABLE 3. Cape Sable Sparrow vocalizations. Asterisks indicate terms from Post and Greenlaw (1975).

Name	Phonetic	Source	Apparent function
Primary song*	"Teedle Chur-eeee-e-e-e-e" "Chee Chur-eeee-e-e-e-e"	male	proclaim territory, attract mate
Abbreviated primary song	"Chur-eeee-e-e" "Eeee-e-e-e"	male	proclaim territory
Whispering primary song	"Chur Chur-eee-e-e-e" (low amplitude)	male	proclaim territory during stress
Subsong*	"Che-eeaahhh"	fledgling	practice of song
Complex flight vocalization*	"Seet, seet,...seet Chur- eeee-e-e-e" "Seet, seet,...seet Chur- eeee-e-e-e Chur-eeee-e-e"	male	proclaim territory
Chip call	"Chip," "Chit," "Cherp," "Cher," "Cheet"	male female fledgling nestling	general purpose, chasing, aggression, nest defense, preening, initiate flight song
Tsip call*	"seet," "sisst" (high frequency)	male female	high state of anxiety, combat, nest defense, initiate flight song
Si twitter*	"Seet, seet,...seet"	male female?	chasing, combat, initiate flight song
Squeaz call	"Squeazz," "Squee," "Squeaa," "Eaah," "Jaaa," "Squeah"	male female? fledgling?	general aggression, chasing
Distress call	"Eeeak," "Eaaah," "Seerp," "Eah"	male female fledgling nestling	proclaim distress
Peep call	"Eeep"	nestling	general communication, food begging?
Cedar call	"Ce-ce-ce-ce-ce....ce"	nestling fledgling	food begging
Seep note*	"Seeet," "Seee"	male female? fledgling	chasing, flocking sound
Miscellaneous vocalizations	"Eurr" "Eoo-ooo-ooo" "Che-che-che...che" "Shu-shu...shu" Melody of musical notes Variable harsh notes	male female male female male? male fledgling	aggression aggression unknown unknown unknown

vidual that has been observed doing little or no singing on a particular day will utter one or more complex flight vocalizations.

Several different vocalizations are associated with chasing; however, only the *squeaz* call is common. It is heard primarily during the later stages of chases. Also associated with threat and combat, it was positively heard only from males.

The *seep* note (Fig. 4) also is heard during chasing, but it is most commonly heard in postbreeding flocks (mostly fledglings). The note is often prevalent near

dark. Because of the somewhat contradictory nature of its two contexts, it might be two different notes that can be distinguished only with special equipment.

When handled, some adults, fledglings, and nestlings emit a distress call that may be equivalent to the *scree* call described by Post and Greenlaw (1975). The *peep* call of nestlings is barely audible and generally is heard from the day of hatching through the fourth day (sixth day for some individuals). On the fifth day it normally is replaced by the "cedar" call, which is named for its similarity to the sound of Cedar Waxwings,

Bombycilla cedrorum. It is associated with feeding at least into the flightless fledgling period. At first, the call is high-pitched, but it gradually becomes slightly lower and hoarser. It might be equivalent to the *chup* call described by Post and Greenlaw (1975).

Several other rarely heard vocalizations have been identified. The sound "eurr" has been heard from adults of both sexes and "eoo-eoo-eoo" was heard only from males. Both appear to be associated with aggression. A series of repetitive notes, "che-che...che," was heard several times from adults, one of which was a female. This may be equivalent to either the *chew* call or the *tchi* vocalization described by Post and Greenlaw (1975). Another vocalization is a series of melodious notes with no apparent pattern. It was first heard from a hand-held male, then, at a later date, was heard once in the field; no function was apparent. Vocalizations are summarized in Table 3.

Territory

Seaside Sparrows exhibit considerable variability in the organization of territories. Territories for *A. m. maritima* have been described as defended areas with separate nesting and feeding areas (Woelfenden 1956, 1968), all-purpose territories (Post 1974), and small grouped territories with a small defended area around the nest and an undefended remote foraging area (Post 1974). However, the Cape Sable Sparrows studied at upper Taylor Slough and Ochopee had only all-purpose breeding territories (Type A of Hinde 1956) within which all mating, nesting, and feeding occur. For the males at the Taylor Slough site, territories tended to remain stationary for later breeding attempts in the same season, and for ensuing seasons. Only 2 of 16 males (12.5%) relocated completely between successive nestings in the same season at Taylor Slough in 1974. Only 2 of the 14 males present at the end of the 1974 breeding season (14%) relocated for the beginning of the 1975 breeding season. At the Ochopee site, one male retained the same territory for three consecutive breeding seasons.

Based on measurements of 62 territories, Cape Sable Sparrows defend from 0.3 to 6.8 ha. At Taylor Slough (1974-1976) 52 territories ranged from 0.3 to 6.6 ha (mean = 1.4 ha). At Ochopee, 10 territories ranged from 0.7 to 6.8 ha (mean = 3.6 ha). Though territories tended to be stationary, their borders did fluctuate. As a breeding season progressed, some territories expanded, but most contracted. At Taylor Slough in 1974, the mean size of 16 territories decreased about 20% from 2.0 to 1.6 ha. The amount of seemingly acceptable habitat incorporated into breeding territories varied extensively between breeding seasons. In the southern segment of the Taylor Slough site, in 1974, 13 territories occupied 25.1 ha. In 1975, 18 territories occupied only 16.6 ha. Thus the number of territories increased 38%, but the space occupied by the sparrows decreased 34%. Although the space available for each territory decreased 53% from 1.9 to 0.9 ha, mean territory size decreased only 44% from 1.6 to 0.9 ha. The additional males of 1975 set up their territories mostly along the periphery of the area occupied in 1974 (Fig. 36 in Werner 1975).

The model for Cape Sable Sparrows establishing territories in *Muhlenbergia* prairie appears to function

as follows. The sparrows begin to inhabit the prairie 1 to 2 years after it burns, establishing territories on the optimum sites. During succeeding years, as more sparrows immigrate and some that hatched locally remain to breed, competition for nesting territories increases. As a result, territories decrease in size, and the most recent arrivals tend to occupy suboptimal sites adjacent to the earlier residents. By the third breeding season after the fire, little alteration in community structure occurs. By the fourth breeding season, few, if any, of the original residents remain. The vegetation becomes slightly decadent (Wade et al. 1980) as suspended mats of dead grass accumulate in the tussocks. The biomass of live vegetation appears to decline, lowering production. Both time and condition of the fuel increase the probability of fires. As the residents die or disperse, few adults replace them. Density becomes low and territories large. Some areas apparently fail to sustain the sparrows. When the area burns again, some of the population may be destroyed; most individuals should escape. A year or two later, the cycle begins again.

Aggression between neighboring males is a common occurrence at Taylor Slough. However, disputes are so rare among the Big Cypress and Cape Sable populations that they were once believed to be nonterritorial (Stimson 1968). At Ochopee, territories overlapped as much as 45 m. Males commonly were observed in the area of overlap and occasionally used the same perch to sing, though not at the same time. Once, at the Fox Lake prairie, two singing males flew to the same perch where they remained quiet for about 1 minute, after which they flew away from each other and resumed singing. Chasing was observed several times at Ochopee, and at least once both participants were singing males. Chasing also occurred on the Fox Lake prairie, but the sex of the participants was not determined.

Bobbing, similar to that described by Post and Greenlaw (1975) for Northern Seaside Sparrows, was observed once in an *Eleocharis* slough at Ochopee. The two birds stood face-to-face. One individual raised its head and body while the other crouched. This sequence was repeated several times; sometimes their heads rose together. Between periods of head bobbing the more active individual moved left and right of the less active individual. *Tsip* calls were emitted during the performance. The two individuals moved into the *Spartina*. Wing fluttering and *si* twittering ensued, followed by *squeaz* calls. The two parted and sang. This encounter took place after sunset, and the sexual identity of the participants was not established. However, we suspect both were males engaged in a territorial boundary dispute.

At Taylor Slough, territorial disputes are particularly common during March, April, and May. Chases generally are short and occasionally end with both males together in the grass. The *squeaz* call usually is emitted in flight, though other vocalizations sometimes are given, especially the *seep* note. Chases generally are short. However, once when a bachelor male attempted to displace a neighboring, mated male with fledglings, long chases lasting over 1 minute ensued. Only an occasional *seep* note by the chasing male broke the silence while the two flew in circles over the territory. After 2 days, the aggressor took the territory, and the former resi-

dent moved slightly west. The female continued to feed her fledglings and was not known to mate with the new male. When two males are on the ground together, the *squeaz* call is common, especially at initial contact. *Tsip* and *chip* calls also are common and *si* twittering occasional. These notes usually are followed by a short period of quiet after which one or both males depart to their respective territories.

Primary song near a neighbor's territory frequently leads to a face-to-face encounter along the territory boundary. Generally, aggressive acts occur on the ground; but opponents occasionally have aerial combat above the vegetation. Sometimes one male will attack another male on its song perch. Contact appears frequent, though sometimes only *chip* calls are exchanged, and the males remain several meters apart. After an encounter, males often are observed preening.

Occasionally, a singing male initiates whispering primary song at the approach of another male. The singing male extends its wings upward over its body and appears to vibrate them, as described for the nominate race by Post and Greenlaw (1975). *Si* twittering and *squeaz* calls sometimes are emitted between periods of whispering primary song. If the aggressor departs, normal singing resumes; if not, the defender often chases. Sometimes the aggressor initiates combat. Other times, when two singing males approach each other, one changes to whispering primary song, while the other retains full primary song, usually without combat. Sometimes both become quiet.

Pair Bond

Often Cape Sable Sparrows retain the same mate for successive nest cycles, but some individuals change. In 1974 a pair that completed one nest cycle successfully, separated thereafter. The male moved and appeared unmated the remainder of the breeding season. The female moved to the territory of another male, who was believed to have been mated previously. The new pair completed two more nest cycles that year, and they were together the following year on the same territory. Some males fail to pair for an entire breeding season. Some of these succeed at pairing later. For example, one male that was unmated throughout 1974 was mated to an unbanded female in 1975. At the Taylor Slough study site, 12% of the males appeared to remain bachelors throughout the breeding season in 1974 and 11% in 1975. As many as 22 to 31% were believed to be bachelors during some part of the breeding seasons during 1974 and 1975.

Except for chasing, observations of interactions between males and females are rare. Once, at Ochopee, a pair was seen facing one another. The male paced right and left before her several times. Afterwards, they disappeared into the grass for about 5 minutes. Several times thereafter, when she flew, he followed. On several occasions, females near males appeared to extend or partially extend their wings and vibrate them. One individual was observed not only extending both wings, but also fluttering them along the side of her body. This behavior resembles the female copulatory display described by Post and Greenlaw (1975) for the nominate race.

Males appear to chase females as often as they

chase males. Often it is difficult for a female to fly any distance without being pursued and followed into the grass by a male. Several times males, already shy of mist nets, were captured because they followed their mates too closely. The *squeaz* call often is associated with the chase, but some chases are silent. Chasing occurs during the nest cycle at least until incubation.

Nest and Eggs

At the Taylor Slough study site, nests normally are built in a tussock of grass, usually *Muhlenbergia filipes*. Occasionally unclumped graminoid vegetation, especially *Cladium jamaicense*, and unclumped *Muhlenbergia* are used as support for the nest. At Cape Sable, nests were reported in both Switchgrass, a clumped grass, and in Salt Grass, a short matted grass (Nicholson 1928, Stimson 1968). Active nests never were found in *Cladium* or *Spartina* prairies. Only twice were adults observed carrying nesting material; one was a female, the other was of unknown sex.

Cape Sable Sparrows construct both cupped and domed nests. One cup nest at Taylor Slough was built under a shelf of dead grass. This also was reported on Cape Sable (Nicholson 1928). Once, dead grass, which was part of the tussock, was fashioned dome-like over a cup nest. During the 1973, 1974, and 1975 breeding seasons, 16 nests were located at Taylor Slough; of these, 44% were domed and 56% were cupped.

The departure azimuth was recorded to the nearest 45° for all nests located in 1974 and 1975. For the domed nests, 67% had the entrance facing an easterly direction, and the mean departure azimuth was 135°. The mean departure azimuth for cup nests was 257°, and 71% had a westerly departure azimuth. This appears to be caused by the orientation of the habitat and how the nest is attached to the vegetation. The grass leaned predominantly toward the west. The more rigid upright grass was on the east side of the clump. Orienting the nest orifice of domed nests toward the east provided the sturdiest anchor for the entrance while retaining optimum cover. Vegetation surrounding cup nests was most open toward the west, thus facilitating departure westward. Cup nests often list slightly (estimated 10°) on the approach side as the nest cycle progresses; however, listing is not known to have caused any nest failures.

Though the cup nest was the type most frequently described for other races, references to arched (Nicholson 1928) and canopied (Tomkins 1941) nests for Dusky and MacGillivray's Seaside Sparrows demonstrate that other members of the species may build nests of both types.

At Taylor Slough, nests were composed principally of woven *Muhlenbergia*. Entrances for domed nests varied from a narrow slit to fairly round structures. The lower inside portion of all nests was lined with very fine grass. Early descriptions of nest composition on Cape Sable state that they were made of dead marsh grass with a fine grass lining, and some nests were partially covered by dead grass (Nicholson 1928). An old nest located at the Fox Lake study site, believed to be that of a Cape Sable Sparrow, was composed of *Eleocharis cellulosa* on the outside; with *Spartina bakeri*, the principal component, on the inside. The inside of this cup nest was lined with what appeared to be very narrow por-

tions of *Spartina* leaves. The nest was situated in the lower part of a *Spartina* tussock. Measurements were within the range found at Taylor Slough.

At Taylor Slough, nests were 6 to 37 cm above the substrate (mean = 18 cm, N = 16). Outside diameter of the nest cup was 8 to 13 cm wide (mean = 10 cm, N = 15) and 4 to 11 cm high (mean = 7 cm, N = 15). Domed nests were 7 to 19 cm high (mean = 13 cm, N = 6). The inside of the nest cup was 4 to 7 cm in diameter (mean = 6 cm, N = 15) and 2 to 7 cm deep (mean = 5 cm, N = 15). The cavity inside domed nests was 6 to 9 cm high (mean = 7 cm, N = 6). However, measuring from the orifice to the back of the nest, the cavity was 5 to 14 cm long (mean = 8 cm, N = 7). The entrance to domed nests was 3 to 6 cm high (mean = 4 cm, N = 6) and 2 to 4 cm wide (mean = 3 cm, N = 6). Nests weighed 8 to 24 gm (mean = 16 gm, N = 15), oven-dried. Nests were used only once.

Cape Sable Sparrows normally lay three to four eggs, perhaps sometimes only two. However, as many as five have been reported on Cape Sable (Howell 1932). At Taylor Slough, 50% of the nests (N = 16) contained four eggs or nestlings, 44% contained three eggs or nestlings, and 6% contained two nestlings. The nominate race has been reported to have as many as six eggs with a normal clutch of four or five eggs (Woolfenden 1956).

The eggs have one of two base colors, a very light blue or a light grayish beige. All are heavily marked with reddish-brown spots. Most eggs in one clutch are the same color; but at least 12% of the nests contained eggs with both base colors. Of 27 eggs examined, 70% were light blue, the remainder grayish beige.

The mean size of 27 eggs at Taylor Slough was 19.3×14.7 mm; the eggs showing the extremes for length measured 20.6×14.6 mm and 17.6×14.4 mm; for width they were 18.7×15.2 mm and 19.9×14.1 mm. Stimson (1968) reported a mean of 19.9×15.1 mm for eggs, probably from Cape Sable. The mean weight of the eggs 9 days prior to hatching was 2.3 gm (N = 14). Four days later, these eggs averaged 0.3 gm less, a 13% reduction in weight. The eggs in one clutch of four had a mean weight of 1.9 gm 4 days prior to hatching. The mean weight of three eggs that failed to hatch was 1.9 gm.

No nest was discovered before completion of the clutch, so the incubation period remains unknown, although it is known to exceed 11 days. MacGillivray's Seaside Sparrow is reported to have an incubation period of about 12 days (Sprunt 1968), and the Dusky Seaside Sparrow between 12 and 13 days (Trost 1968). The Cape Sable Sparrow probably is similar.

The female develops a single median vascularized brood patch. Attendance at the nest varied considerably between different individuals. Some parents were on the nest during 73% of the observer's visits and generally flushed when a person was within 2 to 4 meters of the nest. Other parents were never seen on the nest. Females appear to be absent most frequently during midday. Males normally continue to sing during the morning and evening until the eggs hatch. Some parents make *chip* and *tsip* calls when humans are near the nest, others remain silent.

Of 55 eggs at Taylor Slough, four were taken by a predator (7%), and nine more failed to hatch (18% of remaining 51 eggs). Only one unhatched egg was exam-

TABLE 4. Neossoptile placement on nestlings (N = 5).

Location	Mean	Range
Capital tract		
Superciliary region	7.8/side	6-10/side
Occipital region	3.0/side	—
Spinal tract		
Dorsal region (anterior)	5.7/side	5-6/side
Dorsal region (posterior)	1.6	1-2
Pelvic region	5.2	4-6
Humeral tract	3.5/side	3-5/side
Femoral tract	7.1/side	6-8/side
Alar tract	7.2/side	6-8/side
Ventral tract		
Abdominal region	7.0/side	6-10/side

ined; it revealed no evidence of an embryo. Unhatched eggs remain in the nest as the nestlings develop and mysteriously disappear when they fledge. Whether unhatched eggs are removed by the parents or eaten by predators remains unknown.

Based on a sample of one, hatching seems typical of passerines. The shell split in a circle around the widest part of the egg, forming two parts; extension of the body moved the shell apart, freeing the chick. Parents apparently remove the empty shells immediately after hatching, as no fragments were found in nests.

Nestling Growth and Development

At hatching the altricial nestlings have only a few neossoptiles (Table 4). The Cape Sable Sparrow nestlings examined had fewer neossoptiles than reported for the Northern Seaside Sparrow (Woolfenden 1956, 1968), but growth and development are similar for both races.

At age day 0, the nestlings are clumsy, and they lie prostrate in the nest. The egg tooth is prominent and remains visible until after fledging. A ridge of tissues extends across the eye where the eyes will open. The abdomen is distended. During the following days, the large abdomen gradually becomes less obvious. The nestlings generally beg when the nest is bumped, and sometimes emit a very faint *peep* call.

At age day 1, papillae are visible on the capital, humeral, and alar tracts and on the cervical and dorsal regions of the spinal tract. On a few individuals, papillae were visible on the crural tract and the cervical region of the ventral tract. At this age the nestlings were able to maintain an upright posture when begging by resting on their tarsi. The *peep* call is more audible than previously.

At age day 2, papillae are visible on all regions of the capital and spinal tracts. On some individuals, papillae begin to appear on the femoral tract. The papillae on the crural and ventral tracts increase. A slit in the eye ridge is obvious, and on some individuals the eye is partly open. When the nest is bumped, begging is intense, and *peep* calls are frequent.

At age day 3, papillae are present on the caudal tract and all regions of the ventral tract. Papillae are

prominent in all pterygiae. The eyes of most individuals are partly open, and the *peep* call is less common than previously. Some individuals begin to cower.

At age day 4, the papillae on the crural tract are more prominent and the eyes open farther.

At age day 5, the eyes are generally fully open. However, on some nestlings eye development is not complete until the following day. The cedar call is heard and associated with begging. A slight buff or rufous color begins to appear on the spinal, femoral, crural, alar, and ventral tracts. A yellowish tinge begins to appear near the alula of some individuals.

At age day 6, nestlings beg intensely. Cowering begins to predominate when they are approached. On some individuals, some of the teleoptiles begin to break through their sheaths on all but the capital tract.

At age day 7, nestlings first give the *chip* call. Many more teleoptiles break through their sheaths, including primaries and part of the capital tract. Breast streaking begins to appear. The nestlings are more mobile and some can perch moderately well.

At age day 8, nestlings are fairly well feathered, except for the coronal region of the capital tract. The breast streaks are distinct, and a light edge is present on the scapular feathers. The nestlings tend to be active, though not yet agile. Some nestlings disappeared and were believed to have fledged on this day.

At age day 9, nestlings can run well. Only a few neosoptiles remain on the well-feathered bodies. Most young appear to fledge on day 9 to 10, but some do not fledge until the day 11. Fledging was verified by subsequent observations for only two nests with known-age young; of the six nestlings, four fledged on day 10 and two on day 11. Even though some nests contain nestlings that vary in age by at least a day, the entire brood tends to fledge on the same day. Of 41 nestlings from 16 nests, 31% definitely fledged (25% of the nests). An additional 45 % of the young (44% of the nests) probably fledged, but were not observed afterwards. An additional 7% of the young (6% of the nests) may have fledged, but the young disappeared from the nest earlier than normal and were not seen again. Five percent of the young (5% of the nests) probably failed because of predation. For 12% of the nestlings (19% of the nests), failure through predation was certain.

Specific measurements of nestling growth are summarized in Table 5. Although other measurements increased throughout the nest cycle, the width of the mouth increased to a maximum mean size of 12.2 mm at age day 5 and then gradually decreased to adult size. At its maximum, the mouth width of nestlings surpassed adults by 39%.

Throughout the nest cycle, the parents maintain a clean nest. Fecal sacs were never seen in or near the nest. Woolfenden (1956) reported that adult Northern Seaside Sparrows removed sacs from the nest and deposited them at the foraging grounds.

Both parents feed young. When with nestlings, males normally sing very little or not at all. The food carried by the parents appeared to be primarily lepidopteran larvae and orthopterans. The delivery rate appeared to be about four to six trips per hour. This is only about one-third the delivery rate reported for the nominate race (Post 1974); however, delivery rate is difficult to

estimate because parents usually become preoccupied with human observers when people are in the territory. Parents will not fly directly to the nest when humans are in the territory. Some parents landed a distance from the nest and approached it on foot; others would continue to make *chip* and *tsip* calls and eventually swallowed or lost the food, which they carried at the rear of the bill behind the tooth at the angle on the mandibular tomium. Adults were seen feeding young up to 10 days after fledging.

Some parents become secretive and silent after the young fledge; others continue to give *chip* and *tsip* calls when intruders are present. Some males show a distinct increase in singing with the termination of a nest cycle, others initiate successive nest cycles without obvious changes in behavior.

Some breeding cycles apparently overlap, in that a new nest is constructed while dependent fledglings from the previous brood still exist. Evidence for this comes from one pair that fledged a second brood exactly one month (31 days) after the first brood fledged. A normal breeding cycle should take more time (care of eggs, 12-13 days; of nestlings, 9-11 days; and of fledglings, ca. 10 days). One female that changed mates fledged the succeeding brood 48 days later; the third successive brood, which was with the same (second) mate, was fledged less than 37 days later. Another pair fledged successive broods without changing mates with a 38-day interval.

No individual appeared to be more than triple brooded, and many appeared to be only double brooded. However, third broods could have been overlooked. The duration of the breeding season during some years would permit more than three broods if that is physiologically possible. Flightless fledglings have been observed as early as 2 April, in 1975, indicating that the beginning of that nest cycle was in late February. Eggs have been found (though destroyed by predators prior to hatching) as late as 7 July 1974, and nestlings seen as late as 26 July 1974 indicate nest cycles that would have terminated in the early part of August. Thus the potential breeding season slightly exceeds 5 months. In 1975 the prairie flooded in early July, and breeding appeared to terminate then.

The breeding season extends through environmental extremes varying from the severest part of the dry season far into the rainy season. During the middle of the day in the dry season, both nestlings and adults can be seen panting. The rainy season is marked by heavy convectional showers, lightning, and strong, gusting winds. Examination of two nests immediately after one such storm revealed that they had been covered during the storm, because the nest cups and the fledglings were dry.

Fledglings

When approached, flightless fledglings usually freeze on their grassy perch and hold the position until the human is less than a meter away. As the approach distance continues to close, the fledgling attempts to flee by running. Fledglings appear to be capable of short flights at about age 17 days. Fledglings barely able to fly were observed in one territory 17 and 18 days after hatching; however, the identity of the individuals

TABLE 5. Nestling, fledgling, and adult measurements.

Age	Days after hatching											Ftl	Fledg*	Fly	Fledg*	Ad. male	Ad. female
	0	1	2	3	4	5	6	7	8	9	10						
Culmen (mm)																	
Mean	3.7	4.0	4.8	5.6	6.3	7.0	7.5	8.0	8.3	9.0	9.6	10.1	13.8	14.5	13.9		
Range	3.3-	3.1-	4.3-	5.3-	5.7-	6.6-	7.0-	7.6-	7.6-	8.6-	9.5-	—	—	13.5-	13.2-		
	4.0	4.5	5.3	6.2	6.9	7.4	7.9	8.3	9.0	9.5	9.6			16.1	14.6		
N	8	7	7	7	7	7	8	10	5	4	2	1	1	23	11		
Distance from tip of bill to nares (mm)																	
Mean	1.8	2.3	2.6	2.8	3.2	3.7	4.0	4.4	4.7	4.9	5.2	5.7	9.4	10.1	9.8		
Range	1.4-	2.0-	2.3-	2.4-	3.0-	3.4-	3.7-	4.1-	4.1-	4.8-	5.0-	—	—	9.4-	9.4-		
	2.2	2.7	2.8	3.2	3.6	4.1	4.4	4.7	5.0	5.0	5.5	—	—	10.6	10.0		
N	8	7	7	7	7	7	8	10	5	4	2	1	1	17	7		
Bill depth (mm)																	
Mean	2.8	3.0	3.3	3.4	3.6	3.8	4.0	4.2	4.0	4.1	4.6	4.5	6.8	6.5	6.4		
Range	2.4-	2.6-	2.8-	2.9-	3.1-	3.5-	3.5-	3.6-	3.8-	3.8-	4.6-	—	—	6.0-	5.9-		
	3.2	3.5	3.9	4.0	4.2	4.3	4.6	4.8	4.4	4.4	4.7			7.2	6.8		
N	8	7	7	7	7	7	8	10	5	4	2	1	1	22	10		
Maximum mouth width (mm)																	
Mean	8.2	—	10.9	11.5	12.0	12.2	12.0	11.8	11.7	11.4	10.7	11.8	9.4	8.9	8.7		
Range	7.6-	—	10.7-	11.3-	11.6-	11.8-	11.7-	11.4-	11.4-	11.0-	—	—	—	8.3-	8.1-		
	8.5		11.0	11.9	12.4	12.4	12.3	12.3	12.3	12.1				9.3	9.1		
N	4	0	3	3	3	3	3	3	3	3	1	1	1	4	3		
Tarsometatarsus length (mm)																	
Mean	8.1	10.0	12.6	15.0	17.8	20.6	22.2	23.4	23.5	24.8	25.0	25.9	24.9	25.1	24.6		
Range	6.9-	9.3-	11.3-	12.9-	15.7-	18.7-	20.8-	21.3-	22.0-	24.0-	25.0-	—	—	24.0-	23.8-		
	8.7	10.8	14.0	16.8	19.4	21.8	22.9	25.1	24.8	25.5	25.1			26.7	25.6		
N	8	7	7	7	7	7	8	10	5	4	2	1	1	23	11		
2nd primary length (mm)																	
Mean	0	T**	0.6	3.0	6.9	11.9	15.6	19.5	23.7	28.0	30.4	32.3	43.3	44.8	41.8		
Range	0	0-T**	0.2-	0.8-	4.4-	8.9-	12.9-	14.8-	19.8-	26.6-	29.9-	—	—	43.5-	40.6-		
			1.6	5.1	9.6	14.4	19.1	24.6	28.1	29.4	30.8			46.3	43.4		
N	8	7	7	7	7	7	8	10	5	4	2	1	1	13	6		
8th primary length (mm)																	
Mean	0	T	1.0	3.1	7.5	10.7	14.4	16.8	19.2	23.2	24.0	26.7	42.3	43.7	41.2		
Range	0	T	0.7-	2.2-	7.2-	9.1-	10.9-	12.6-	15.7-	21.6-	23.1-	—	—	42.6-	38.9-		
			1.5	3.8	7.8	12.2	18.0	22.9	22.9	25.3	24.8			44.9	42.6		
N	4	3	3	3	3	3	4	6	5	4	2	1	1	8	4		
2nd rectrix length (mm)																	
Mean	0	0	0	T	T	0.3	1.3	2.4	3.3	5.8	7.4	9.2	41.2	48.1	44.8		
Range	0	0	0	0-T	T	T-	0.6-	0.6-	1.2-	4.0-	6.6-	—	—	45.1-	43.1-		
						0.6	2.2	4.0	5.7	7.5	8.1			53.3	47.5		
N	8	7	7	7	7	7	8	10	5	4	2			13	6		
Weight (gm)																	
Mean	2.3	3.7	5.6	7.3	9.7	11.6	12.4	13.8	13.4	13.6	15.0	15.6	17.6	19.4	17.9		
Range	2.0-	2.9-	4.4-	5.7-	8.4-	10.2-	10.8-	11.2-	12.4-	13.0-	14.8-	—	16.4-	17.7-	16.2-		
	2.6	4.5	6.4	8.5	11.2	12.9	14.1	15.5	15.0	14.7	15.2		20.2	22.7	19.0		
N	9	7	7	7	7	7	9	12	5	4	2	1	9	28	12		

* FtlFledg = flightless fledgling; FlyFledg = fledgling capable of flight.

** Trace

was not verified. On another occasion, a flightless fledgling was captured. Measurements indicated that it probably was no more than 11 or 12 days old. Three days later it was observed flying several meters and was positively identified as the same individual. As the fledglings developed, they began to acquire yellow lores similar to the adults. The mean weight of fledglings ($N = 9$) was 7% less than adult weights ($N = 40$). Even though young began to fledge as early as March, flying fledglings were rarely observed before June. From June onward through July, fledglings were seen frequently.

Occasionally, fledglings were seen being chased by adults. The chase was often short. On the occasions when participants were identified, an adult male and an unrelated fledgling were involved. Whether females chase fledglings and whether parents chase their own fledglings of previous broods could not be determined. Fledglings have been observed following adults carrying food. The adult generally ignored the fledglings; however, this might have initiated some chases. Once a fledgling was seen chasing another fledgling. Adults have flown to fledglings captured in a mist net, landing within several meters of the captured bird. The adult appeared to have come to assist the distressed fledgling, but the purpose was not clear.

Though occasionally alone, fledglings generally occur in groups of two to seven. Often an adult is with them. The *seep* note is commonly heard in the flock. Some flocks appear to frequent certain areas. The area in which a flock travels may be much larger than a normal territory. Activities of the fledgling flock often center around physical features generally ignored or avoided by breeding adults, such as willow bushes, tiny tree islands (several meters in diameter), or a tall stand of Sawgrass growing in a solution hole. One young individual was seen repeatedly in the same general place for 13 days. Eleven days later it was seen about 200 m north. Another juvenile was captured about 600 m south of where it had fledged about 7 weeks earlier; 32 days later it was seen several hundred meters farther north, and the following year it established a territory about 850 m north and slightly west of where it was last captured. Observations of marked fledglings indicate that the flock is not always composed of the same individuals. In 1973, nine fledglings were marked at a site frequented by a fledgling flock. Afterwards, only two marked juveniles were observed, one time each, at the same site. The size of the flock appeared to remain about the same, but its constituency was different.

Of those fledglings marked in 1973, only two (22%) were observed in the study area in 1974. One established a territory about 400 m to the south of where it was marked; the other was a female captured about 940 m south of where it was marked. In 1974 only 4 of 22 young (18%) believed to have fledged were observed as fledglings in the study site; only one of those (25%) was seen in the study site in 1975. This bird represents 4% of the original marked nestlings and 3% of the eggs observed in all known nests that year. The remainder died, emigrated, or were unobserved. Postbreeding emigrations of fledglings probably provide the principal mechanism of dispersal, for the adults tend to remain stationary.

Molt and Preening

By the middle of July, fledglings acquiring the new, dark body feathers were common. One fledgling seen on 2 September 1974 appeared to be in full first basic plumage. At the same time, some other fledglings appeared to be molting.

Cape Sable Sparrows molt only once annually. Adults do not appear to begin the prebasic molt until August or September. On 2 September 1974 an adult was observed with a short tail and dark plumage. By 15 September its tail appeared to be fully grown. After the prebasic molt, the adults appear very dark dorsally, with distinct yellow lores, white underparts, and dark breast streaks. By the beginning of the breeding season, feather wear is obvious and the color appears slightly lighter than in the fall. As feather wear continues, the adults lose color contrast (photograph in Werner 1978) and become lighter dorsally and grayer ventrally than at the beginning of the breeding season (photograph in National Fish and Wildlife Laboratory 1980). Throughout the breeding season, occasional new replacement feathers are observed. A few missing rectrices are common among males. One male lost his entire tail between 24 March and 1 April 1974. By the end of May, the tail appeared normal.

Preening is one of the few activities commonly performed on an exposed perch, especially early in the morning when the grass is wet. Singing frequently is interrupted for several minutes by preening. Occasionally an adult preens while making *chip* calls. Periodically during preening, the rectrices are fanned open slightly and wagged back and forth. The head is scratched by moving the foot over the slightly extended wing.

HISTORY

The Cape Sable Sparrow is the most isolated of all races of the Seaside Sparrow. Its range is about 260 km from the nearest population of *Ammodramus maritimus peninsulae* on the Gulf Coast and 280 km from the nearest population of *A. m. nigrescens* on the Atlantic Coast of Florida. The Cape Sable Sparrow also differs most from the other races in its choice of habitat, which is essentially freshwater prairies. The occasional Seaside Sparrow migrants from the north (probably *A. m. maritimus*) when they reach South Florida, occur in different habitat, namely *Batis* prairie near or adjacent to the Gulf of Mexico. Even the close congener, the Sharp-tailed Sparrow, *Ammodramus caudacutus*, when wintering in South Florida, is more common in *Batis* prairie, although it does occur sympatrically with the Cape Sable Sparrow in the slightly brackish *Spartina* prairies. Based on our knowledge of its habitat, a question arises: How did the Cape Sable Sparrow come to reside in seasonally dry, essentially freshwater prairie habitat?

Beecher (1955) addressed the much broader question of the origin of all races of both species of salt-marsh sparrows, genus *Ammodramus*. He postulated that the races of the Seaside Sparrow owe their initial isolation to river drowning as glacial meltwater was returned to the sea in postglacial time, which eliminated salt marshes at these localities. He also suggested that any races that evolved prior to the last glacial period prob-

ably were eliminated by subsequent glacial periods. Our information on the unique habitat preferences of the Cape Sable Sparrow suggests that this race developed in a manner different from that posed by Beecher. Our ideas also suggest modifications to the postulated origin of all the races.

During interglacial periods tropical climates prevailed in the southern United States (Mengel 1964, Brooks 1974), and sea level was 5 to 30 m higher than at present (Brooks 1973). These conditions favored replacement of any existing temperate graminoid coastal prairies (salt marshes) with tropical mangrove swamps, as typifies South Florida and many tropical coastal areas today. Where the terrain was flat, as in South Florida today, the prairies retreated inland before the spreading mangroves. Elsewhere the mangroves adjoined interior forests, eliminating the prairies to which Seaside Sparrows are restricted. Farther north along the Atlantic Coast, where temperate climates persisted through interglacial periods, preventing mangroves from becoming established, Seaside Sparrows continued to survive in coastal marshes.

When the continental glaciers began to grow, sea level began receding; the climate became cooler, and temperate coastal prairie spread southward as the mangroves died out. With more of the flat terrain of the continental shelf exposed, salt marshes suitable for Seaside Sparrows probably became extensive. Current temperature (Thomas 1974) and phytogeographical distribution suggest that winter temperatures no more than 3-5°C cooler than today would have been adequate to extend temperate graminoid prairies around the entire South Florida coast where low-energy shorelines existed. Certainly early in the glacial cycle, temperatures declined this much. Gates (1976) estimates that July air temperatures in peninsular Florida reached 11°C lower than today during the Wisconsin glacial maximum.

When the seas fell to present-day levels, the flat coastal marshes of Florida probably interdigitated with the receding mangroves, as they do now during the present temperate conditions. Further recession exposed the steeper edge of the continental shelf, first at the southern tip of Florida along the Florida Straits, later on both the Atlantic and Gulf Coasts of the peninsula. Now coastal marsh habitat dwindled as it became dissected by high-energy shoreline. Once sea level fell to 40 to 60 m below present levels, all of Florida's Atlantic and southern coastline was on the edge of the continental shelf. Even the persistence of a narrow band of marsh seems unlikely.

During the Wisconsin glacial maximum, sea level fell to about 160 m below present-day levels (Ballard and Uchupi 1970) and reached the edge of the continental shelf. Then, even the Gulf Coast of Florida had a steep shoreline. Coastal prairies probably existed only as isolated marshes between extensive stretches of high-energy coastline. The high, cool interior of Florida was drier (Fairbridge 1974), but the drainage basins were larger. Some had small deltas (Ballard and Uchupi 1970). We suggest these river basins with their deltas and presumed salt marshes, isolated from each other by high-energy coastline were the refugia, and not the barriers, for Seaside Sparrows. Thus, in contrast to Beecher's (1955) hypothesis, differentiation took place

during the recent glacial maximum instead of the preceding interglacial inundation. We suggest that *A. m. sennetti* originated in the Rio Grande delta, *A. m. fisheri* in the Mississippi delta, *A. m. juncicola* in the Apalachicola delta, *A. m. peninsulae* in the Suwannee-Withlachoochee delta, *A. m. mirabilis* in the Shark River delta, *A. m. nigrescens* somewhere in eastern-central or southern Florida, *A. m. pelonota* in the St. Johns delta, and *A. m. macgillivraii* and *A. m. maritima* in regions along the Atlantic Coast north of Florida.

Brooks (1973) suggested naming the Recent (Holocene) the "Age of Estuaries." Estuaries, that is drowned river valleys, which have been an uncommon feature during most of the earth's history (Russell 1967), today constitute a high percentage of the world's coastline. Their appearance following the last glaciation, and persistence since then, is attributable to sea levels moving up onto the gentle slopes of the continental shelves, a process that began about 14,000 to 18,000 B.P. (Milliman and Emery 1968, Fairbridge 1974, Gates 1976). During the process, shoreline marshes probably spread out from the estuaries and joined those from adjacent estuaries. Gene flow between the previously geographically isolated sparrow populations probably increased. Any major recessions in sea level during the general trend of flooding could have isolated marshes and their sparrows.

As sea level along the Gulf Coast of Florida neared the steeper lands of the central ridge of the peninsula, an effective barrier to salt marshes formed between Tampa Bay estuary and Cape Romano to the south. Furthermore, because the climate was warming, mangroves replaced the diminishing marshes. Only in the vast flat Everglades did remnants of prairie habitat remain landward of the encroaching mangroves. We postulate these conditions isolated pre-*Ammospiza maritima mirabilis* from its relatives, and forced it inland into freshwater prairie.

Evidence for the existence of freshwater prairies where saline mangrove communities now stand is strong (Craighead 1971, Gleason et al. 1974). Some investigators suggest that about 6,000 years B.P. sea level was similar to that of today, and that it then fluctuated over a range of several meters through four periods of minor transgression and regression (Fairbridge 1974). Others suggest that at 6,000 B.P. the sea was several meters lower than today and that it has risen constantly to its present level (Scholl et al. 1969). Though soil cores indicate that some transgression has occurred (Gleason et al. 1974) since the Wisconsin, the mangroves apparently never extended much farther inland than currently.

At present the Cape Sable Sparrow is divided into three isolated populations. This probably occurred as the birds were forced inland north and south of Shark Slough basin in advance of the encroaching mangroves. The Cape Sable population probably was separated more recently from the Taylor Slough population by mangrove encroachment across the narrow eastern neck of the Cape Sable peninsula. Vestiges of the prairie that once connected this population to those farther inland still are present. Some gene flow may continue to occur between the Big Cypress and Taylor Slough populations, as the Shark Slough marshes probably are not as formidable a barrier as mangrove forest, especially

during severe drought and possibly after catastrophic events such as hurricanes and large fires.

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An Annotated Bibliography of the Seaside Sparrow

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An all-inclusive bibliography for any bird species can only be attempted, never truly completed. In my search for significant Seaside Sparrow references, I believe that I have found all major works on *Ammodramus* *maritima* as well as most minor references (e.g. notes, distributional information from regional works). All of the citations in this paper were checked for correctness, and read (unless cited as "not seen"). A few general works, such as field guides, were deliberately omitted. From modest beginnings, the number of Seaside Sparrow citations grew to over 200, covering a period of more than 150 years.

The original citation for each subspecies is noted, and these references are summarized in Table 1. Worth noting is that most papers incorrectly cite Robert Ridgway's original description of the Dusky Seaside Sparrow. This paper was actually written by Spencer F. Baird and Ridgway (see Baird and Ridgway 1873, below). For a complete list of the various name changes for each subspecies, the reader is referred to Hellmayr (1939) and to the A.O.U. Check-list and its Thirty-second and Thirty-fourth Supplements (A.O.U. 1957, 1973, 1982). The last of these, which appeared after the

date of this symposium, moved the Seaside Sparrow from the genus *Ammodramus* to *Ammodramus*.

ACKNOWLEDGMENTS

I am greatly indebted for the patient help from Jeffrey A. Cox and Thomas Webber in the preparation of this bibliography. Oliver L. Austin Jr., James L. Baker, Herbert W. Kale II, Willard P. Leenhouts, William Post, and the Inter-Library Loan staff of Hume Library, University of Florida, aided significantly in helping me find the originals of many papers that were difficult to locate.

ANNOTATED LIST OF CITATIONS

- Allen, Joel A. 1888a. Descriptions of two new subspecies of the Seaside Sparrow (*Ammodramus maritimus*). Auk 5:284-287. — Original descriptions of Scott's and Texas Seaside Sparrows.
- Allen, Joel A. 1888b. Further notes on Seaside Sparrows. Auk 5:426. — Compares six specimens of *Ammodramus maritimus sennetti* and *A. m. peninsulae*.

TABLE 1. Dates and references for original descriptions of subspecies of the Seaside Sparrow (*Ammodramus maritimus*).

- Ammodramus maritimus maritimus* Wilson 1811, p. 68.
Ammodramus maritimus macgillivraii Audubon 1834, p. 285.
Ammodramus maritimus nigrescens Baird and Ridgway 1873, p. 198.
Ammodramus maritimus penninsulae Allen 1888, p. 284.
Ammodramus maritimus sennetti Allen 1888, p. 286.
Ammodramus maritimus fisheri Chapman 1899, p. 10.
Ammodramus maritimus howelli Griscom and Nichols 1920, p. 22 (synonymous with *A. m. fisheri*).
Ammodramus maritimus juncicola Griscom and Nichols 1920, p. 25.
Ammodramus maritimus mirabilis Howell 1919, p. 86.
Ammodramus maritimus waynei Oberholser 1931, p. 125 (synonymous with *A. m. macgillivraii*).
Ammodramus maritimus pelonota Oberholser 1931, p. 126.
Ammodramus maritimus [sic] *shannoni* Bailey 1931, p. 1 (synonymous with *A. m. pelonota*).

- American Ornithologists' Union. 1957. Check-list of North American Birds (5th ed.), p. 595-597. American Ornithologists' Union, Baltimore. 691 p. — The 1957 fifth edition lists seven subspecies of *Ammospiza maritima* and considers *A. nigrescens* and *A. mirabilis* to be distinct species. (These two species were changed to subspecies in the Thirty-second Supplement, 1973).
- American Ornithologists' Union. 1973. Thirty-second supplement to the American Ornithologists' Union Check-list of North American Birds. Auk 90:411-419. — Changes *A. nigrescens* to *A. m. nigrescens* and *A. mirabilis* to *A. m. mirabilis*.
- American Ornithologists' Union. 1982. Thirty-fourth supplement to the American Ornithologists' Union Check-list of North American Birds. Supplement to Auk 99(3):1-16CC. — Changes *Ammospiza maritima* to *Ammodramus maritimus*.
- Anderson, William. 1942. Rediscovery of the Cape Sable Seaside Sparrow in Collier County. Florida Nat. 16:12. — Cape Sable believed to have been extirpated until Anderson found a population in the Big Cypress Swamp in 1942.
- Anes, Shelia L., F. Enders, and F. Heath. 1966. Breeding-bird census: Ditched salt marsh. Amer. Birds 20:660-661.
- Anonymous. 1980. Sun sets on the Dusky Seaside Sparrow. BioScience 30:576. — Short account of recent history of Dusky.
- Antonio, Frederick B., and J. Ellis. 1981. History and current status of the Dusky Seaside Sparrow. Amer. Assoc. of Zool. Parks and Aquariums Regional Conf. Proc. 1981:57-66. — Brief history of the Dusky; describes housing and care of the five captive Dusky males at the Teaching Zoo of Santa Fe Community College (Florida).
- Appleberry, Edna L. 1949. Field notes and news. Chat 13:77. — Seaside Sparrow nest with three eggs, Wilmington, N.C., 15 May 1949.
- Arnow, Isaac F. 1906. The Seaside Sparrow nesting in bushes. Auk 23:226. Observed and collected a few nests of *A. m. macgillivrayi* in shrubs (mostly Sea Myrtle) east of St. Mary's, Georgia.
- Audubon, John J. 1831. Ornithological Biography, Vol. 1, p. 470-472. Adam and Charles Black, Edinburgh. 512 p. — Description and breeding habits of "The Seaside Finch" (*Fringilla maritima*).
- Audubon, John J. 1834. Macgillivray's Finch. Ornithological Biography, Vol. 2, p. 285-286. Adam and Charles Black, Edinburgh. 588 p. — Original description of *A. m. macgillivrayi* as *Fringilla macgillivrayi*.
- Audubon, John J. 1838. Ornithological Biography, Vol. 4, p. 394. Adam and Charles Black, Edinburgh. 618 p. — Habits of "Macgillivray's Finch" (*Fringilla macgillivrayi*).
- Audubon, John J. 1849. [i.e. 1839]. Ornithological Biography, Vol. 5, p. 499-500. Adam and Charles Black, Edinburgh. 664 p. — Description of the palate and internal anatomy of *A. m. macgillivrayi*.
- Audubon, John J. 1967. The Birds of America, Vol. III, p. 105-107. Dover Publications, Inc., New York. 233 p. — A Dover republication of Audubon's 1840 - 1844 octavo edition, which appeared in 100 parts. Description of the behavior and voice of the "Seaside Finch" and "Macgillivray's Shore Finch."
- Austin, Oliver L., Jr. 1966. Banding Seaside Sparrows in South Carolina. EBBA News 29(3):112. — Unusually high spring tides near Beaufort, S.C., forced *A. m. macgillivrayi* from the marshes onto a tiny hammock. Banded 120 of these birds and netted 34 birds the following year, 10 of which were returns.
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- Austin, Oliver L., Jr. 1968b. Smyrna Seaside Sparrow. Pages 835-838 in Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. A. C. Bent (O. L. Austin Jr., editor). U.S. Nat. Mus. Bull. 237. Washington, D.C. 1,889 p. — Life history, distribution, habits, vocalizations, and predators of *A. m. pelonota*.
- Bagg, Aaron C., and S. A. Eliot Jr. 1937. Birds of the Connecticut Valley in Massachusetts. Hampshire Bookshop, Northampton, Mass. 813 p. — Footnote on page 634 is the first report of a Seaside Sparrow nest being parasitized by the Brown-headed Cowbird (*Molothrus ater*).
- Bailey, Harold H. 1913. The Birds of Virginia, p. 227. J. P. Bell Co., Inc., Lynchburg, Va. 362 p. — Range and some breeding behavior of the Northern Seaside Sparrow in Virginia.
- Bailey, Harold H. 1925. The Birds of Florida, p. 104-106. Williams and Wilkins Co., Baltimore, Md. 146 p. — Brief descriptions and distribution information for the Dusky, Cape Sable, Scott's, Louisiana, and MacGillivray's Seaside Sparrows in Florida.
- Bailey, Harold H. 1931. A new Seaside Sparrow from Florida. Bull. No. 7. Bailey Mus. Nat. Hist., Miami, Fla. [1] p. — Publication dated "1 August 1931" [= 2 Dec. 1931]. Described *Thryospiza maritimus* [sic] *shannoni*, now considered to be synonymous with *A. m. pelonota*.
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- some new forms of American birds. *Bulletin of the Essex Institute* (Salem, Mass.) 5(12):197-201. — Original description of Dusky Seaside Sparrow as *Ammodramus maritimus* var. *nigrescens*. This reference often erroneously cited as "Ridgway 1873."
- Baird, Spencer F., T. M. Brewer, and R. Ridgway. 1874. *North American Birds*, Vol. 3: Land Birds, p. 513-514. Little, Brown and Company. 560 p. — Short description of a "remarkable new local form" of Seaside Sparrow, the Dusky Seaside Sparrow; color plate of the Dusky in Vol. 1, facing p. 560.
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- Baker, James L. 1978. Status of the Dusky Seaside Sparrow. Georgia Dept. Nat. Res. Tech. Bull., p. 94-99. — Population trends and reasons for decline of *A. m. nigrescens* until 1978; suggestions for management.
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- Beckett, Ted. 1969. MacGillivray's Seaside Sparrow, in *Briefs for the Files*, James F. Parnell, editor. *Chat* 33:107. — Reports new nesting site for race in Muddy Bay near Georgetown, S.C.
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- Bull, John. 1964. *Birds of the New York Area*. Harper & Row, N.Y. 540 p. [Not seen.]
- Bull, John. 1974. *Birds of New York State*. Doubleday/-Natural History Press, Garden city, N.Y. 655 p. [Not seen.]
- Burleigh, Thomas D. 1937. Bird life on the North Carolina coast. *Auk* 54:452-460. — Distribution of MacGillivray's Seaside Sparrow in North Carolina mentioned (p. 460).
- Burleigh, Thomas D. 1944. The bird life on the Gulf Coast region of Mississippi. *Occas. Pap. Mus. Zool. Louisiana State Univ.* 20:324-490. — Distribution of *A. m. howelli* and *A. m. fisheri*.
- Burleigh, Thomas D. 1958. *Georgia Birds*, p. 656-662. Univ. Oklahoma Press, Norman, Okla. 746 p. — Ranges and comments on behavior for the Northern, MacGillivray's, and Smyrna Seaside Sparrows.
- Carleton, Geoffrey. 1958. The birds of Central and Prospect Parks. *Proc. Linnaean Soc. New York* 66-70:1-60.
- Carter, Joseph H., III, and James F. Parnell. 1976. TV tower kills in eastern North Carolina. *Chat* 40:1-9. — Seaside Sparrows occurred at these inland sites during fall migration for three consecutive years.
- Chamberlain, W. David. 1978. The birds of Turtle Island, S.C. *Chat* 42:3-7. — List based on unpublished field records of Ivan R. Tomkins. Seaside Sparrow a breeding bird (p. 5); no details given.
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- Chapman, Frank M. 1899. The distribution and relationships of *Ammodramus maritimus* and its allies. *Auk* 16:1-12. — Chapman examined 160 Seaside Sparrow specimens from several collections, representing: *A. m. maritimus*, *A. m. peninsulae*, *A. m. macgillivrayi*, *A. m. nigrescens*, and *A. m. sennetti*; proposed that the Seaside Sparrows from Louisiana be a distinct subspecies; original description of *A. m. fisheri*.
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- Chapman, Frank M. 1927. *Handbook of Birds of Eastern North America* (rev. ed.), p. 393-395. D. Appleton and Co., New York. 530 p. — Plumage, molt, and range of five subspecies of "Meadow-chippies."
- Choate, Ernest A., and J. d'Arcy Northwood. 1969. Forty years of Christmas Bird Counts in Cape May County [N.J.]. *Cassinia* 51:3-10. — Sharp-tailed and Seaside Sparrows seen almost every year; high counts 55 and 17, respectively.
- Cody, Martin L. 1968. On the methods of resource division in grassland bird communities. *Amer. Nat.* 102:107-147. — Mentions Seaside Sparrow foraging in relation to habitat.

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- Cooke, Wells W. 1910. The migration of North American sparrows. *Bird Lore* 12:111-112. — Several records for Seaside Sparrows, 1892-1904.
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- Cutts, Ernest. 1960. Seaside Sparrow, in *Briefs for the Files*, B. R. Chamberlain, editor. *Chat* 24:105. — Nest and four eggs 17 May 1960, young 22 May, Charleston County, S.C.
- Delaney, Michael F., Willard P. Leenhouts, Beau Sauselein, and Herbert W. Kale II. 1981. The 1980 Dusky Seaside Sparrow survey. *Florida Field Nat.* 9(4):64-67. — No Dusksies found in 1981 (April 29 - June 19) 75-man-hour survey.
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- Dwight, Jonathan, Jr. 1898. The Sharp-tailed Sparrow (*Ammodramus caudacutus*) and its geographical races. *Auk* 13:271-278. — Song of the Sharp-tailed Sparrow resembles "choking gasp" of a Seaside Sparrow.
- Dwight, Jonathan, Jr. 1900. The sequences of plumages and moults of the passerine birds of New York, p. 190-193. *Ann. New York Acad. Sci.* 13:73-760. — Molt pattern for *Ammospiza* sp.
- Eberhart, Jonathan. 1968. The dwindling Dusky. *Sci. News*. 93:501-502. — Status (as of 1968); management possibilities.
- Elliot, John J. 1962. Sharp-tailed and Seaside Sparrows on Long Island, New York. *Kingbird* 11:115-123. — Twenty years of natural history observation on *A. caudacuta caudacuta* and *A. m. maritima* around Long Island, N.Y.; saw a partially albinistic *A. m. maritima* in the fall of 1940.
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- Enders, Frank. 1970. The double-scratch in the Seaside Sparrow. *Wilson Bull.* 82:225. — First report of a Seaside Sparrow performing the "double-scratch."
- Enders, Frank, and W. Post. 1971. White-spotting in the genus *Ammospiza* and other grassland sparrows. *Bird-banding* 42:210-219. — Partial albinism observed in Sharp-tailed and Northern Seaside Sparrows on Long Island, N.Y. Did not find white-spotting in any of the other subspecies of Seaside Sparrows examined in the American Museum of Natural History collection.
- Fables, David, Jr. 1955. Annotated List of New Jersey Birds, p. 70. Urner Orn. Club, Newark, N.J. 95 p. — Distribution of *A. maritima* in New Jersey.
- Faxon, Walter. 1897. What is *Fringilla macgillivraii* Aud.? *Auk* 14:321-322. States that the Louisiana Seaside Sparrow is not *A. m. macgillivraii*.
- Finnley, Dona (editor). 1980. Future of Dusky May Depend on Captive Propagation. *Endangered Species Tech. Bull. Special Rept.*, Vol. 5 (April):1-6. U.S. Fish and Wildlife Serv., Washington, D.C. 6 p. — Account of the events leading to the decline of the Dusky; management suggestions.
- Forbush, Edward H. 1929. *Birds of Massachusetts and Other New England States, Part III: Land Birds from Sparrows to Thrushes*, p. 65-67. Mass. Dept. of Agric., Norwood Press, Norwood. 466 p. — Good summary of the field marks, molts, behavior, and distribution of the Northern Seaside Sparrow.
- Forbush, Edward H., and J. B. May. 1939. *Natural History of the Birds of Eastern and Central North America*, p. 513-516. Houghton Mifflin & Co., Boston. 554 p. — Range and behavior of the Northern Seaside Sparrow; also mentions MacGillivray's, Dusky, Cape Sable, Scott's, Wakulla, Howell's, and Louisiana Seaside Sparrows.
- Friedmann, Herbert. 1949. Additional data on victims of parasitic cowbirds. *Auk* 66:154-163. — Cowbirds rarely "penetrate" brackish or salt water, thus Seaside Sparrows seldom parasitized. One known account of cowbird parasitism, originally reported in Bagg and Eliot (1937).
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- Grey, John H., Jr. 1941. The breeding birds of Pea Island [N.C.]. Chat 5:50-54. — MacGillivray's Seaside Sparrow common breeder; young in nest 28 May 1941.
- Griscom, Ludlow. 1944. A second revision of the Seaside Sparrows. Occas. Pap. Mus. Zool. Louisiana State Univ., No. 19:313-328. — In this "second revision" Griscom examined more than 200 skins from several collections and reviewed the literature to date on the Seaside Sparrow subspecies. *A. m. howelli* is reduced to synonymy with *A. m. fisheri* and *A. m. waynei* to synonymy with *A. m. macgillivrayi*. Griscom recommends that *A. nigrescens* remain a separate species and that *A. mirabilis* be reduced to subspecific rank.
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- Griscom, Ludlow, and D. E. Snyder. 1955. The Birds of Massachusetts: An Annotated and Revised Check List, p. 238. Peabody Mus., Salem, Mass. 295 p. — Distribution of the Northern Seaside Sparrow in Massachusetts.
- Hellmayr, Charles E. 1938. Catalogue of Birds of the Americas and the Adjacent Islands, Part XI, p. 507-512. Field Mus. Nat. Hist. Zool. Ser., Vol. XIII, Part XI. 662 p. — Catalogue for specimens of *A. m. maritima*, *A. m. macgillivrayi*, *A. m. peninsulae*, *A. m. howelli*, *A. m. fisheri*, and *A. m. sennetti* in the Field Museum of Natural History.
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Vocalization Repertoire of a Marked Population of Seaside Sparrows

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Abstract. Scott's Seaside Sparrow (*Ammospiza maritima peninsulae*) vocalizations, recorded during the breeding and postbreeding season of 1981 near Cedar Key, Florida, are described and discussed. The vocalizations of 39 color-marked (or otherwise individually identified) males, as well as some females, nestlings, and juveniles, were recorded and analyzed. Primary song, countersinging, flight songs, subsongs, and 10 different calls were recorded. The occurrence and intensity of these vocalizations were influenced by modifying factors such as weather, presence of other birds, and time of year.

Various investigators have reported their observations on the singing behavior of the Seaside Sparrow (*Ammospiza maritima*), usually in the form of incidental general behavioral notes (Saunders 1951, Peterson 1947, Stone 1937, Tomkins 1941, Sprunt 1924, Howell 1932, Kopman 1915, Lowery 1955, Norris 1968, Nicholson 1946, Trost 1968, Holt and Sutton 1926, Borror 1961).

Relatively recent studies by Woolfenden (1956), Werner (1975), and Post and Greenlaw (1975) have included more thorough descriptions of the vocalizations and associated behavior of these birds. Previous to our study, most descriptions have been of the primary song, with the exception of Post and Greenlaw's (1975) excellent work on the vocalizations and displays of a population of Northern Seaside Sparrows (*A. m. maritima*) in New York.

Audubon (as quoted by Sprunt 1968) said flatly that the Seaside Sparrow's song was "impossible to imitate," and described it as a "sort of roll of five or six syllables." This "curious little song" (Howell 1932) has been described as "wheezing," "squeaky," and "chippering" (Howell 1932, Nicholson 1946). More than one author has noted the similarity of the Seaside Sparrow's song to that of the Red-winged Blackbird (*Agelaius phoeniceus*) (Howell 1932, Nicholson 1946).

In this paper I first describe in detail the songs and calls of a population of Scott's Seaside Sparrows (*A. m. peninsulae*) studied intensively during the breeding

and postbreeding seasons of 1981. A second paper by J. W. Hardy follows this presentation, dealing with geographic variation in the primary songs of Seaside Sparrows.

STUDY SITE AND METHODS

William Post began research on the Cedar Key, Florida, population of Scott's Seaside Sparrows in the winter of 1979. Post worked extensively on this population for 2 years. With the termination of his project, in early 1981, I began my study of the vocalizations of these birds as a part of my doctoral dissertation research in the Department of Zoology at the University of Florida.

Scott's Seaside Sparrows are found in salt marshes along the Gulf of Mexico from Pinellas County northward approximately 250 km to Taylor County. The study site borders Waccasassa Bay, approximately 6 km NE of the town of Cedar Key, Levy County, Florida (29°11'N). The topography of this marsh is flat, except for tidal creeks ranging in depth up to 1 m and covering approximately 6% of the study area. The dominant vascular plants are: *Spartina alterniflora* (38%), *Juncus roemerianus* (26%), *Distichlis spicata* (23%), and *Salicornia virginica* (8%).

The study site consists of 35 ha, gridded with wooden stakes placed at 25-m intervals. Wire prongs extend from the stakes to prevent their use by predatory birds. Owing to extensive and wide tidal creeks,

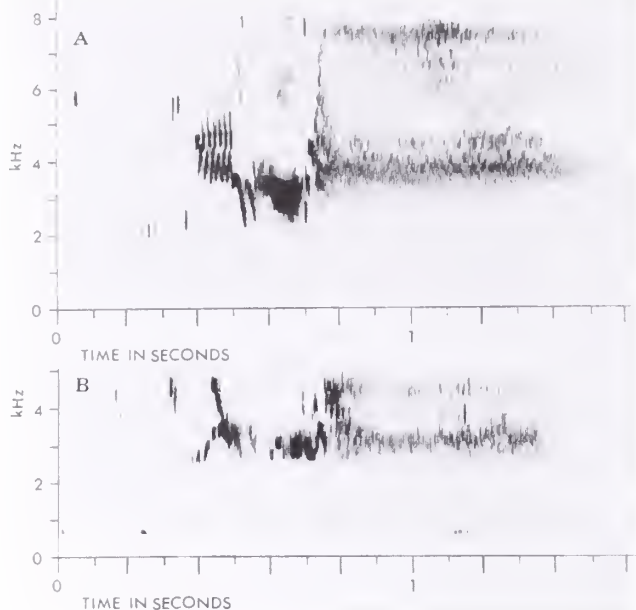


Fig. 1. Scott's Seaside Sparrow sonograms. A, primary song; B, subsong recorded in early fall.

the study area is divided into two units: "Cedar Key East" and "Cedar Key West."

Birds captured throughout the year in 1979 and 1980 were banded by Post with U.S. Fish and Wildlife Service bands and unique color combinations. A few birds escaped our capture efforts; however, their identities were ascertained through the observer's familiarity with their territorial areas, their unique primary songs, or both.

I tape recorded the primary songs of 39 male sparrows as well as other vocalizations from females, nestlings, and juveniles. I recorded primary songs from February through July in 1981; most work was concentrated in April and May. Some individuals were recorded on as many as 12 different occasions.

In the field the color designations and locations of vocalizing birds were noted on tape, along with the recordings of the songs and calls. Territories were later plotted and measured. Sonograms were made and tapes deposited in the Bioacoustics Archive of the Florida State Museum, Gainesville, Florida. Recordings were made mostly on a Sony TC-150 cassette recorder (Mineroff-modified) with a Bell and Howell "Shotgun" unidirectional electret condenser microphone with wind screen. Recordings were analyzed on a Kay Elemetrics 7029A Sona-graph using the wide-band filter and either the 80-8000 Hz or the 1600-16,000 Hz scale.

DESCRIPTIONS OF VOCALIZATIONS

In the following discussion I describe the vocalizations, their context, and any characteristic behavior associated with the songs and calls of Scott's Seaside Sparrows as recorded at Cedar Key in the breeding season of 1981. The vocalization types are presented here in approximate order of their relative frequencies. A few of the call types may be somewhat arbitrarily designated because of intergradations between some

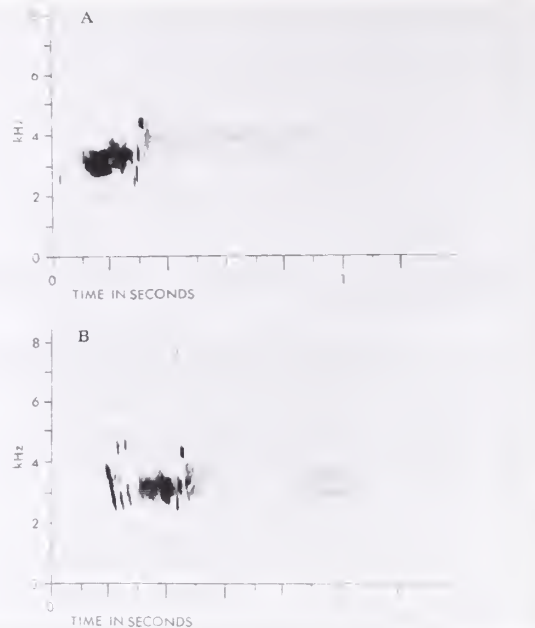


Fig. 2. Scott's Seaside Sparrow sonograms. Primary songs of individuals A and B countersinging.

sounds. (A short recording of these vocalizations is included on side 1 of the phono disc that is part of the published proceedings of this meeting.)

Primary Song

An examination of sonograms of primary song (Fig. 1A) reveals that it is a relatively simple vocalization consisting of one or two (for some individuals) vertical elements followed by a buzzy trill. The song duration of about 1.0 seconds and the frequency range centered generally around 4.0 kHz is characteristic for the entire population.

This vocalization is used in delineating an individual's territory. Only males sing the primary song. The song is usually given from an elevated perch, such as a tuft of *Juncus*. In the 3 years of this study only one male sang from a grid marker stake, although Post and Greenlaw (1975) found that sparrows often sang from their grid markers in a dense population.

Throughout the breeding season, the peak singing activity occurred early in the morning from sunrise to about 3 hours after sunrise. The earliest I heard a bird singing was 20 minutes before sunrise. Some songs were given late in the afternoon until about one-half hour after sunset. I found relatively less evening song activity at Cedar Key than Post and Greenlaw (1975) reported for Northern Seaside Sparrows. The first morning and last evening songs were essentially the same as the songs given during peak morning activity. These first and last songs of the day did seem less "forceful" in quality, and the song rate (songs per minute) was lower very early and late in the day.

Individual males sang two to four song types. A few of the birds had such a distinctive song type within their repertoire that I was able to recognize individuals aurally from as far away as 150 m. A preliminary analysis of my recordings suggested that most song types were shared among males within this population. When

countersinging, the individuals involved usually sang different song types. During a playback experiment an individual bird virtually ignored a recording of his neighbor played at the edge of his territory; however, he responded vigorously to a playback of his own song. One explanation of this reaction is that he had become accustomed to his neighbor's singing but did not recognize his own song.

During the peak of the breeding season, early-morning primary songs were given in bouts of 3 to 5 minutes, interspersed with 1- to 2-minute periods of silence, when the singer sometimes—but not always—changed perches before he resumed singing. In contrast to singing behavior reported in other studies on avian singing and territoriality (Krebs 1977), these Seaside Sparrows did not consistently begin a new song pattern after moving to a new song perch. The singing rate within a bout ranged from about 6 to 9 songs per minute, similar to the rate of 6.6 given for New Jersey birds by Woolfenden (1956) and slightly lower than the 10.6 given for New York birds by Post and Greenlaw (1975). Unmated birds, both bachelors and widowers, sang more intensely than mated birds in my study area.

Countersinging

An individual's song rate sometimes increased noticeably when two birds began countersinging. Countersinging (Fig. 2) was often heard in this population. It usually involved two, but sometimes three and even four birds. The pattern of singing in the song duels was regular: the birds appeared to "take turns" giving their songs, all being given at the same rate. Occasionally the birds' songs would get out of phase with each other and the songs would begin to overlap.

Whisper Song

While aggressive encounters at a distance provoke a higher rate of singing, as described above, the quality as well as the rate of singing is different in close interactions between males within 1 to 5 m of each other. In these close encounters the males sing a muted song at a low rate of 1 to 2 songs per minute. Following Werner's (1975) terminology, I call this the "whisper song" (Fig. 3A). The whisper song is usually given by a bird perched low and hidden in the grass. In contrast to the normal primary song, where the bird throws back his head and opens his beak wide as he sings, the whisper song is given with a closed or almost closed beak. When opponents are visible to each other, the whisper song is often accompanied by aggressive displays such as the raising and quivering of wings.

Flight Song

The flight song (Fig. 4) given by males during the peak of the breeding season is a combination of preliminary calls followed by parts of the primary song. This vocalization is about 3 to 4 seconds long and consists of introductory high-pitched *si*'s, followed by lower pitched *tuck*'s and ending with one or two condensed versions of the primary song. The number, duration, and type of introductory calls vary, and these are given on the ground and during the bird's ascent. The primary song is uttered just before the bird lands.

Almost all flight songs were given in the morning, although a few were given in late afternoon during the

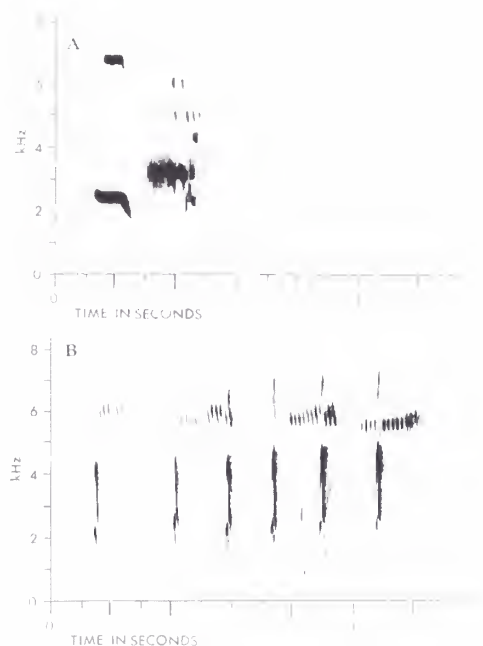


Fig. 3. Scott's Seaside Sparrow sonograms. A, whisper song; B, tuck calls given in flight.

peak of the breeding season. The number of flight songs given per hour varied considerably from individual to individual and from day to day. The most I heard was about one every 10 minutes (all from separate males) within an area of about 4 ha.

Subsong

Young males were observed singing rudimentary subsongs late in July and August (Fig. 1B). This song consists of a garbled warble and parts of the adult primary song. It is not as loud as the primary song and is sung only sporadically. The early subsong progresses to a more advanced subsong occasionally heard throughout the fall and winter. Early in their first spring, these 1-year-old males began to sing more nearly normal primary songs and tried to establish territories.

Other Factors Influencing Singing

Singing, including flight songs and whisper songs, was most intense early in the breeding season (April to early May in 1981 at Cedar Key), before and just after birds were mated. In general, most singing occurred early in the morning, as noted above. However, weather was an important modifier. Very early in the spring birds sang more as the day warmed slightly, up to about 20°C. During the middle and end of the breeding season, increasing heat depressed singing activity up to about 32°C when virtually all singing stopped. Late in the season, birds sang more on cloudy, cool mornings. Brisk winds also significantly reduced singing activity, especially very early in the season. Rain diminished singing only slightly. The numerous calls of other marsh birds, most notably breeding Clapper Rails (*Rallus longirostris*) seemingly had no effect on the Seaside Sparrows. Seaside Sparrows did respond antagonistically toward vocalizing Sharp-tailed Sparrows (*Ammospiza*

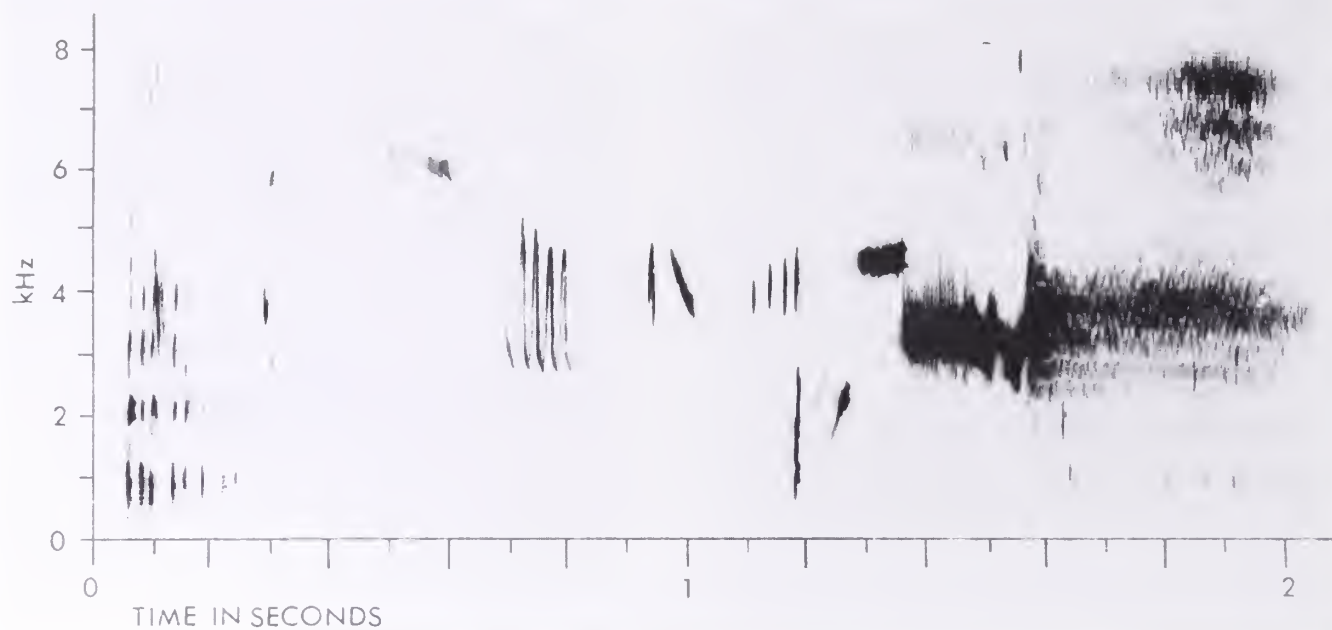


Fig. 4. Scott's Seaside Sparrow sonogram of flight song.

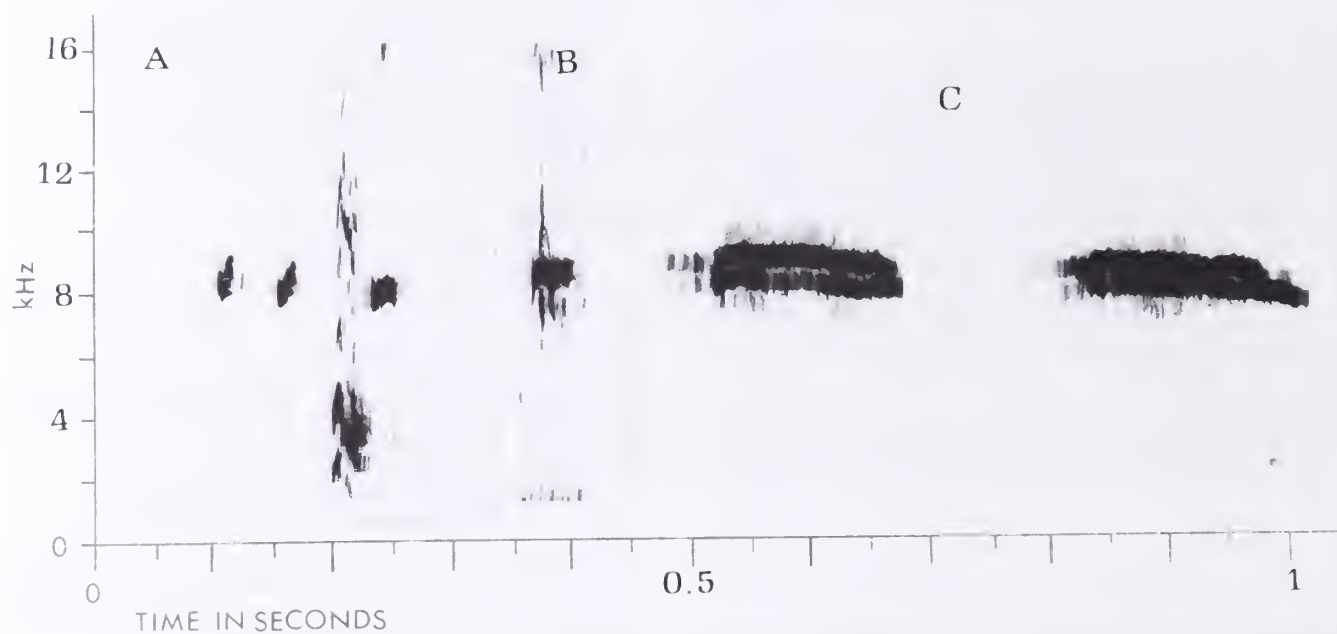


Fig. 5. Scott's Seaside Sparrow sonograms. A, *tuck* and *si* twitters; B, *tsip*; C, *seeep*.

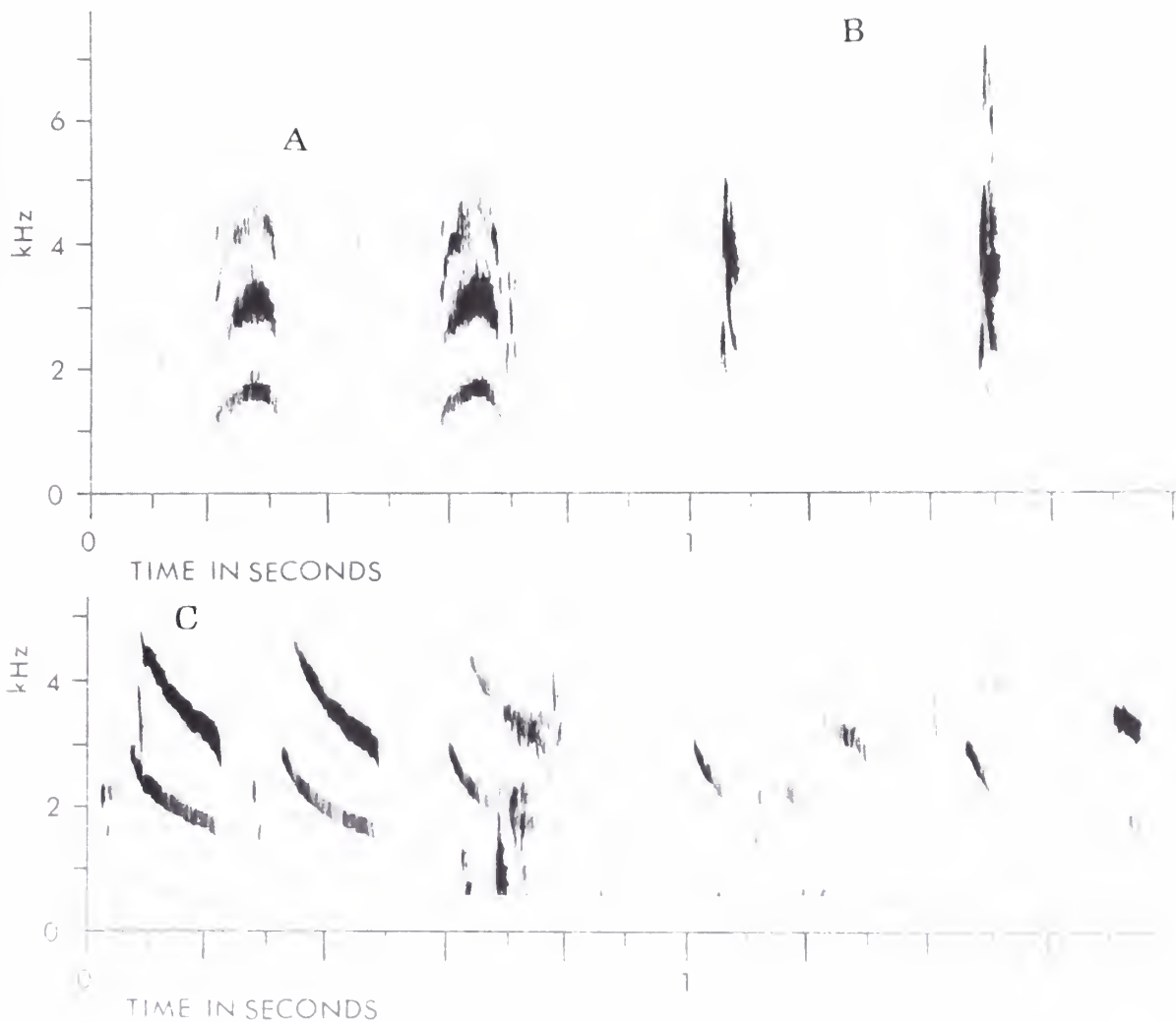


Fig. 6. Scott's Seaside Sparrow sonograms. A, *zuck*; B, *tuck*; C, fast whinny.

caudacuta nelsoni) when these migratory birds were present early in the breeding season.

Calls

Both male and female Seaside Sparrows gave various calls throughout the year. A preliminary analysis of sonograms suggests that the call types described below are essentially the same among all members of this population. Most of these calls have been described in other subspecies of Seaside Sparrows, although a few have not been previously mentioned.

The following is a brief summary of the calls of Seaside Sparrows in approximate order of their frequency during the breeding season. A more detailed description and the contextual nature of these calls is found elsewhere (Post and Greenlaw 1975). I follow the nomenclature of Post and Greenlaw (1975) when possible.

Tuck: The *tuck* (Fig. 3B, Fig. 5A, and Fig. 6B) is a common call given by both males and females. It is a short call covering a wide frequency range. This call is often given during aggressive interactions between birds and also by parents when a human approaches the nest.

Tsip: Both males and females also give the higher pitched, short *tsip* call (Fig. 5B). This call is often

interspersed with *tuck* calls and seems to signify a higher intensity of fear and aggression.

Si twitter: The *tsip* call is sometimes rapidly repeated, thus intergrading into a "si twitter" (Fig. 5A), which is also given along with *tuck* calls by disturbed birds.

Whinny: The "whinny" (Fig. 6C) is a whirling, quavering call that varies in rate. I present fast, normal, and slow whinnies on the record. The whinny is often preceded or followed by the *tchi* vocalization. Post and Greenlaw (1975) report that the whinny is given only by the female and appears to function primarily to attract the mate, although I have also heard males give this vocalization.

Tchi: This short call is somewhat slurred and relatively loud (Fig. 7B). Both sexes use it in a variety of circumstances. The *tchi* is given by flying birds as well as by birds on the ground. In aggressive encounters it accompanies characteristic displays such as the wing raise (Post and Greenlaw 1975).

Zuck: This loud, raspy call is heard most frequently late in the breeding season (Fig. 6A). Although Post and Greenlaw (1975) report that it is usually given in intense fights, my data for Cedar Key indicate that it is usually

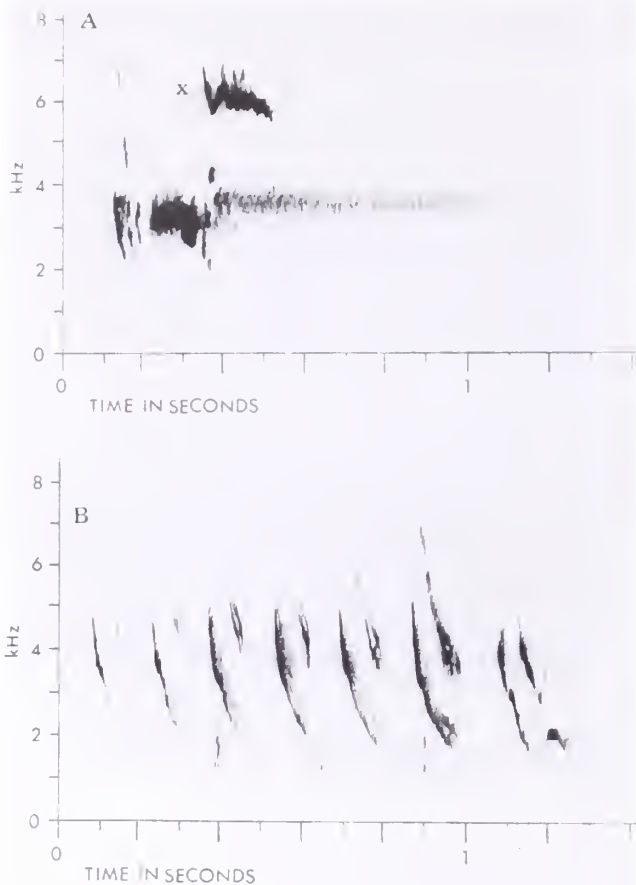


Fig. 7. Scott's Seaside Sparrow sonograms. A, male primary song with female eek imposed (x); B, *tchi*.

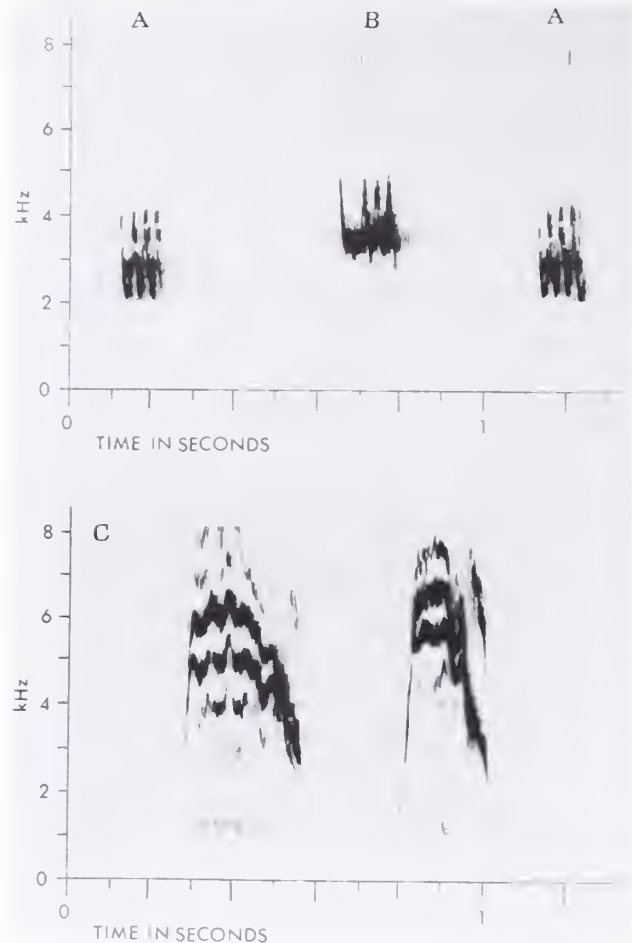


Fig. 8. Seaside Sparrow sonograms. A and B, begging calls from two individual (A and B) captive Scott's x Dusky Seaside Sparrows; C, scree from netted bird in hand.

given on the ground and may also have a social function, as I often heard the *zuck* given by juveniles in small groups and with the parents.

Scree: This harsh call is heard only from birds trapped in mist nets and being handled (Fig. 8C). Both sexes of all ages give this call.

Begging call: The begging call (Fig. 8A and B) was heard in the field. It was also given repeatedly by captive Scott's x Dusky Seaside Sparrow nestlings and fledglings that we hand raised during the summer of 1981.

Chup: Although nestling birds were most often nonvocal, in several instances an older nestling was observed and recorded giving this call, which seemed to function to attract the parents to the nest.

Seep and *eek*. Rarely did I hear a female give what I first designated as the "*eek* response" on the phono record. This call was given at the same time as (Fig. 7A) or following a nearby male's utterance of the primary song. The *eek* is a soft, high-pitched call that is probably a shortened version of the "*seep* note" (Fig. 5C) described by Post and Greenlaw (1975).

ACKNOWLEDGMENTS

I thank William Post for his initial guidance of this project, especially for his assistance in the field and his guiding me to the literature on the Seaside Sparrow. J. W. Hardy contributed substantially by helping with the production of the sonograms and the phonographic record, as well as in making valuable suggestions regarding the manuscript.

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Geographic Variation in Primary Song of the Seaside Sparrow

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It is well known that many bird species exhibit geographic variation in primary song (Thielcke 1969) comparable to, and sometimes correspondent with, morphological variation. The consistency of song from one generation to another in different populations of geographically variable species is apparently not so simply attributable to inheritance, and learning is partly responsible for the generation-to-generation likeness of songs within a population (Nottebohm 1975). Microgeographic variation is found in such forms as the Pacific Coast salt-marsh race of the Savannah Sparrow (*Passerculus sandwichensis beldingi*) (Bradley 1977) in California. This bird inhabits, and is sedentary in, a very patchily distributed habitat. Individuals may grow up and live their entire lives hearing songs only of their own population.

The Seaside Sparrow (*Ammospiza maritima*) is the ecological parallel on the United States Atlantic Ocean and Gulf of Mexico coasts of the Savannah Sparrows studied by Bradley. Most Seaside Sparrow populations are sedentary, only some northern birds of the nominate race having some southward movement in winter (A.O.U. 1957). It seems reasonable to expect that Seaside Sparrows will exhibit much geographic variation in song, including local population dialects.

This paper presents evidence of only the broadest trends in song variation based on recordings made of all races, but not of more than one or two populations of each and of only a few individuals within these. The work necessary to show details of this variation is yet to be done.

General Song Structure

Rapid frequency modulation of Seaside Sparrow song is such that the human ear cannot distinguish all details, except at one-half or one-quarter speed playback of recordings. As one of the results of this fact,

songs from different populations may to us sound very much alike even when they are markedly different. With growing familiarity, however, some features distinguishing different populations do become evident even to human ears. What follows is a description of each of the songs shown in Figures 1 and 2, which depict the sonograms made of these songs. These in turn are in most respects identical or similar to the sounds on the phonodisc that will be enclosed with the proceedings of this symposium.

Terminology

I employ here the basic bird-song reference terms of Davis (1964) in describing and discussing Seaside Sparrow song. Each complete song is thus termed a "phrase" or song phrase. Each song is composed of several "motifs," sequentially arranged and structurally differing segments that in turn compose one or more "figures." The descriptions of these sounds generally follow Bondeson (1977) and include the terms stroke, warble, vibrato, and glissando. The terms note and syllable are usually avoided as they have strict meanings not generally applicable to bird-song description.

RESULTS

Length of Song Phrase

The length of Seaside Sparrow song phrases is not dealt with here in an extensive analytical way. The song phrases shown in the figures range in length from 1.0 to 1.5 sec. The shortest is the song of the Cape Sable (*A. m. mirabilis*), but some phrases of this race range to over 1.2 sec. Songs of Long Island, New York, birds (*A. m. maritima*) range from 1.2 to 1.5 sec. Length appears to vary most with the number of introductory clicks or the degree to which the terminal buzz is sustained. My present judgment is that no significant trend or variation exists in phrase length correlated with geography.

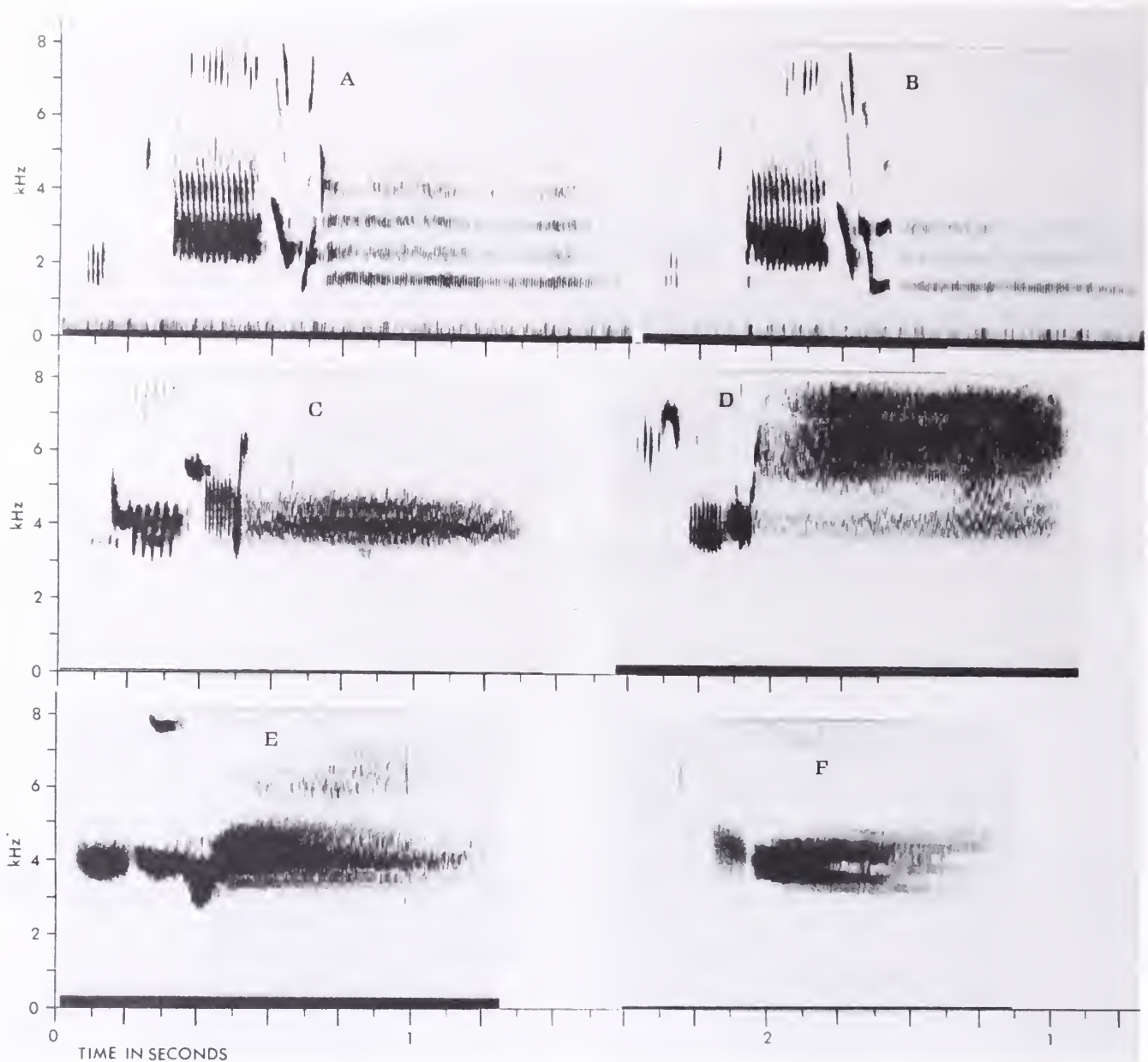


Fig. 1. Sonograms of primary song of five races of Seaside Sparrow. A and B: *A. m. maritima*, Oak Beach marsh, Long Island, New York, 15 May 1971, by W. Post. C: *A. m. maritima*, Deal Island marshes, Somerset County, Maryland, 26 May 1976, by D. S. Lee. D: *A. m. macgillivraii*, near Beaufort, Carteret County, North Carolina, 10 May 1975, by D. S. Lee. E: *A. m. nigrescens*, St. John's National Wildlife Refuge marshes, 18 April 1975, by J. W. Hardy. F: *A. m. mirabilis*, Everglades National Park, Dade County, Florida, 16 April 1975, by J. W. Hardy.

Description of Songs

Song of *A. m. maritima*: Representative of the many recordings made by William Post and Jon Greenlaw on Long Island, New York, this song (Fig. 1 A) is to the human ear one of the most easily distinguishable in this species, because its differences are in pitch rather than modulation. Long Island birds as represented here have much "fuller" sounding songs, richer than songs of other Seasides in frequencies from about 1.5 to 5 kHz in all motifs, from the opening brief trill through the terminal prolonged buzz.

The phrase shown consists of a six-click trill centering on 2 kHz, then a steep glissando figure between 4.5

and 5.5 kHz (heard as a sharp *peep*), the central rapid coarse trill motif at 2 to 5.5 kHz, a motif of two rapid and wide frequency-range warble figures, and finally the terminal prolonged buzz, displaying several comparatively discrete frequency bands. Figure 1 B is a second song type of the same bird; comparing the two shows the degree of variability one can expect among the phrases in a single bout of an individual. The broad frequency range, giving full sound, and the prevalence of sounds below 3 kHz again mark the song. The song also contains an opening series of clicks, a coarse central trill, some complex warble figures, and a low-pitched terminal buzz, although only the buzz is exactly

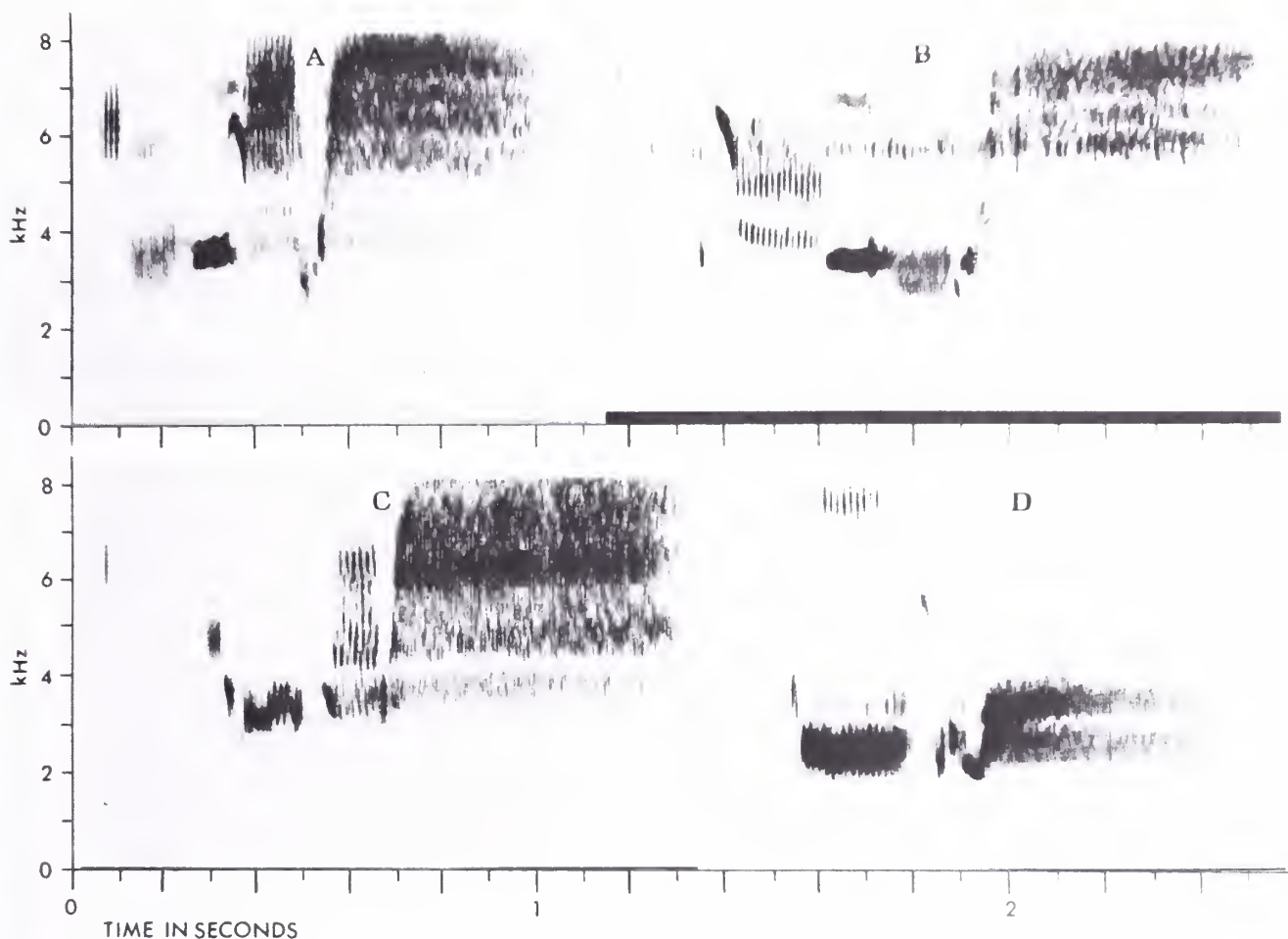


Fig. 2. Sonograms of primary song of four races of Seaside Sparrow. A: *A. m. peninsulae*, Cedar Key, Levy County, Florida, 25 April 1975, by D. S. Lee. B: *A. m. juncicola*, St. Mark's National Wildlife Refuge, Wakulla County, Florida, 21 May 1975, by D. S. Lee. C: *A. m. fisheri*, Dauphin Island, Mobile County, Alabama, 21 May 1976, by D. S. Lee. D: *A. m. sennetti*, Anajuac National Wildlife Refuge, Chambers County, Texas, 27 April 1979, by Ralph Moldenhauer.

like that of the phrase shown in Figure 1 A. Figure 1 C depicts song of a bird of the nominate race recorded in the Deal Island marshes in Maryland. Though the phrase is composed of motifs and figures not unlike those of Long Island birds (again, opening rapid click, coarse central trill, and terminal buzz), a warble figure is almost missing (just at the end of the central trill), and the whole phrase is higher pitched with no portion being below 3 kHz.

Song of *A. m. macgillivraii*: This race (Fig. 1 D) has an even higher-pitched song, no component being less than 3.3 kHz. The terminal buzz and opening motifs are almost completely in the 5.5 to 8 kHz range. Though high-pitched, the introductory series of rapid clicks is emphatic, and there is a coarse central trill ending in a noisy warble before the terminal buzz. Further in contrast to songs of northern birds shown (Fig. 1 A-C), this *macgillivraii* song has as the second figure of its opening motif a tonal or whistled figure in an elliptical shape. I have found no such whistled sounds so far in

birds of the nominate race. As discussed below, such sounds are prominent in Florida Gulf Coast birds.

Song of *A. m. nigrescens*: The race *nigrescens* (Fig. 1 E) possesses a song as distinctive from songs of other Seasides as is this form's plumage. The structure is very simple and mostly noise. The opening rapid clicks described above are replaced by a very rapidly frequency-modulated buzz, barely separated from a rich whistled note, which leads directly into a terminal buzz motif that is mostly concentrated between 3 and 5 kHz and shows very poor definition of any tonal bands like those prominently represented in the songs of birds of the nominate race. My colleague William Post aptly describes the Dusky's song as much more insect-like than most songs of other races.

Song of *A. m. mirabilis*: The race *mirabilis* (Fig. 1 F), the so-called Cape Sable Seaside Sparrow, like *nigrescens*, also has a distinctive song quite unlike that of any other Seaside Sparrow. The song is all noise—even more insect-like than the Dusky's—and consists of

two or three deliberately uttered and more widely spaced clicks (almost like the rapid snapping of fingers), a very rapidly frequency-modulated central buzz, no trill, no warble, and finally a thin terminal buzz with several closely spaced suggestions of tonal centers just above and below 4 kHz. This buzz is so finely modulated as not to show the separate clicks.

Song of *A. m. peninsulae* and *A. m. juncicola*: It is on Florida's west coast along the Gulf of Mexico that birds of the two doubtfully separable races (Post and Kale, pers. comm.) *peninsulae*, the Scott's Seaside Sparrow, and *juncicola*, the Wakulla Seaside Sparrow, live. As can be seen from Figure 2 A and B, the songs of these forms are the most elaborate in the sense of being composed of more motifs and figures that are of considerable sonic variety. Moreover, the songs of these two races are similar to each other. In the *peninsulae* song, recorded at Cedar Key, the introductory portion has not only a rapid series of clicks centering on about 6.5 kHz, but also, immediately following, a rapid buzz centering on about 3.8 kHz. I consider this as two figures of a single motif. There follows a tonal, whistled motif in two figures, first a rising tone ascending from about 3.3 to 3.8 kHz, then the elliptical high-pitched whistled figure rising first to about 6.8 then descending to 5.0 kHz. Thereafter, we see the coarse central trill and a terminal buzz, the formant frequency bands of which are clearly from 5.2 to more than 8 kHz. Note also a faintly tonal connecting figure between the trill and the buzz.

Although the details of the song of *juncicola* (Fig. 2 B), recorded at St. Mark's National Wildlife Refuge, are different from those of *peninsulae* (Fig. 2 A), these two songs are clearly similar in variety of motifs and figures. There are, as in no other Seaside songs thus far examined, two tonal whistled figures, one following the two opening clicks, (the first at 7.5 kHz and the second at 3.5 kHz). Next there is a coarse trill, not centrally located as in other races, then a whistle with a fundamental dominant tone at 7.0 kHz. This is followed by a rapid frequency-modulated buzz centered at about 3.1 kHz, another tonal punctuation, again at 3.5 kHz and linked to the terminal buzz. The energy of the last is concentrated in vague frequency bands in the 7 to 8 kHz range. (A stridulant insect sound is seen just below 6 kHz all the way across the print.)

Song of *A. m. fisheri*: The central northern Gulf of Mexico coast is occupied by the race *fisheri*, which ranges from western Florida to eastern Texas. The song (Fig. 2 C) shown was recorded on Dauphin Island, Alabama. Although it is fairly complex, it is unlike the songs of the two preceding races, in being mostly buzzes and trills, with what seem to be tonal elements being merely punctuations (either suffix or prefix) to buzzes and trills. Thus, the song opens with a single click centered at about 6 to 7 kHz, there is a 0.25-sec pause, a brief coarse buzz, a rapid stroke-vibrato (almost a trill), then a coarse trill punctuated fore and aft by a sharp tonal figure or stroke. The last of these leads immediately to the terminal buzz, the energy of which is concentrated in the 6- to 8-kHz range.

Song of *A. m. sennetti*: The westernmost race of the Seaside Sparrow, *sennetti*, occurs in marshes of coastal

southern Texas. The song shown (Fig. 2 D) has a terminal buzz similar to that of *A. m. mirabilis*, being of comparatively narrow frequency range. This terminal buzz also is notably lower in frequency than the ones discussed above, except the Long Island, New York, birds of the nominate race with the lowest-pitched buzz. The song of *sennetti* depicted (Fig. 2 D) is constructed as follows. The opening motif is of three deliberate, low clicks, followed by an up-down glissando tone that is a prefix to a coarse trill, which has a fundamental formant frequency band centered at about 2.6 kHz. These could be artifacts of recording and reproduction, but at 7.5 to over 8.0 kHz there is an emphatic repetition of the fundamental; it could be a third harmonic of the dominant fundamental. Following the trill there is a vaguely tonal figure of roughly warbled structure, the final portion of which is linked to the terminal buzz.

CONCLUSIONS AND SUMMARY

Seaside Sparrow songs are more complex than the human ear can easily detect and are composed of a variety of sonic characters. These include clicks, buzzes, trills, and tonal figures, which are whistled sounds taking the form of up-down glissandi, warbles, strokes, and constant-pitch notes, sustained for up to 60 msec. Generally, a song opens with a short rapid trill or two or three deliberate clicks at about 40-msec intervals. Most songs have a more or less centrally located terminal buzz, but its pitch and noisiness vary. Birds of Long Island marshes have the lowest-pitched buzzes followed by those of southern Texas. Only the Long Island birds thus far are known to be distinguishable by pitch of utterance. Dusky and Cape Sable Seasides have the simplest songs, composed only of clicks and buzzes.

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Microgeographic Distribution of Breeding Seaside Sparrows on New York Salt Marshes

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Abstract. Seaside Sparrows (*Ammospiza maritima*) on Long Island, New York, are largely confined to the extensive salt marshes behind the barrier beaches along its southwestern shore. Many marshes in this area, especially those covered with relatively short grasses, are not used by Seasides. In suitable marshes they occur in low to high densities, depending on marsh characteristics. Their patchy distributions on Long Island salt marshes are clearly related to identifiable physiognomic characteristics of the marsh vegetation, and to the spatial dispersion of patch types. This relationship seems to arise largely from the behavioral tendencies of Seasides to nest above water levels in dense clumps of persistent grasses early in the breeding season and to feed in relatively open spots where they have access to mud substrates, ground litter, and the bases of rooted grass culms. The sparrows are sufficiently opportunistic that they are able to occupy quite different marshes as long as their nesting and feeding dependencies are met. High-marsh territories are large and contain a high diversity of microhabitats. Nesting and feeding areas tend to be spatially separated, and the territories are often overdispersed. Low-marsh territories tend to be small and contiguous, typically exhibiting spatial overlap between neighbors. Feeding and nesting sites usually are interdispersed in a fine-grained pattern. Aerial photographs showing grass types, occurrence of clumps of grasses and patches of *Iva*, and presence of openings make it possible to predict in a general way the unique distributions of Seaside Sparrows on marshes in the region.

No terrestrial animal is randomly distributed with respect to the patchiness of local or regional environments within its range of occurrence. Such distributions would violate the "jack of all trades, master of none" principle that leads selection in a competitive world to favor the enhanced efficiencies of resource exploitation and energy budgeting stemming from some degree of specialization. Long aware of this fundamental pattern, biologists often have been interested in how organisms distribute themselves among habitats within their ranges.

Recent approaches to this problem for birds living in relatively complex habitats employ ordination and multivariate techniques (e.g. Bond 1957, James 1971). These studies and others highlight the importance of plant-life form and vegetative structure for understanding the ecological distributions of bird species.

In contrast, the Seaside Sparrow (*Ammospiza maritima*) offers a striking opportunity to assess its habitat relations using a simple mapping method. This is possible because salt marshes where it occurs along the north-

east Atlantic Coast are notable for the distinct patchiness of their vegetation in relation to relatively small variations in elevation and to the position of mosquito ditches. The spatial heterogeneity of these marshes, which involves only a comparatively few species of plants, is conspicuous to an observer on the ground and in high-resolution aerial photographs. Moreover, Seaside Sparrows occupy only certain marshes and, on those that they do use, they occur only in certain places. Recent intensive work on the behavior and ecology of northeastern Seasides (Woolfenden 1956, Post 1974, Post and Greenlaw 1982) provides a basis for considering the vegetative patchiness of these marshes in association with the ways that the sparrows use the different patches.

In this paper, I seek to identify specific microhabitats that appear to determine the presence of Seaside Sparrows on salt marshes on Long Island, New York. The dependence of Seasides on certain parts of the vegetation mosaic in these marshes may explain the frequent reference in the literature (e.g. Nicholson 1928,

Key to Abbreviations and Symbols Used in Figures and Tables

MICROHABITATS:

I	<i>Iva frutescens</i> , often associated with patches of salt-meadow grasses.
M	Areas of mud.
MPL	Mud pool, a persistent area (usually small) of shallow, standing water on a muddy bottom.
P	<i>Phragmites australis</i> stand.
PAN	An open area with exposed, saline mud and scattered <i>Salicornia</i> sp. and dwarf <i>S. alterniflora</i> ; panne.
PSC, PSE, PSM	Persistent (dead) culms of <i>Spartina alterniflora</i> that are either semi-erect and clumped (PSC), erect and mostly separated (PSE), or matted and flattened a few centimeters above the substrate (PSM).
s,m,t Sa	Short (dwarf), medium, and tall ecophenes of <i>S. alterniflora</i> .
SM	Salt-meadow grasses, especially <i>S. patens</i> and <i>Distichlis spicata</i> .
W	Wrack deposited by spring and storm tides on the marsh.

SPECIAL SYMBOLS:

4-letter sequences on territories (Fig. 10) represent color-band combinations of occupant males.

Ø, represents an unbanded male on territory.

1946; Tomkins 1941) to their "colonial" habit and may shed light on the sensitivity of their population to habitat modification.

SALT MARSHES ON LONG ISLAND

Long Island is a narrow island of glacial origin that extends parallel to the southern New England shoreline from Manhattan and Staten Island on the west to its easternmost extremity at Montauk Point, a distance of approximately 175 km (110 miles). To the north are Long Island Sound and New England, and to the south is the Atlantic Ocean. Pleistocene glaciations have left two major morainal deposits on the northern portion of the island. As a result, the coastline facing Long Island Sound is relatively steep with numerous bluffs and headlands, and salt marshes consequently are localized and small. These marshes, which typically occur in protected spots within bays and in the mouths of drowned stream and river valleys, are largely of the type known as "high marshes" where salt-meadow grasses (*Spartina patens*, *Distichlis spicata*) dominate. *Iva frutescens*, a low shrub, occurs near upland margins of the marshes and also along some ditches on them. *Spartina alterniflora*, or Smooth Cordgrass, tends to be restricted in extent along tidal channels and in frequently flooded spots that offer little opportunity for Seaside Sparrows to nest or feed. Although Sharp-tailed Sparrows (*A. caudacuta*) commonly occur in summer on these north-

shore marshes, the Seaside Sparrow today is rare and extremely local there as a summer resident (Elliot 1962, Bull 1974, pers. obs.). Similarly, it is rare and local or absent on the eastern end of Long Island.

The southern part of Long Island is a flat, sandy outwash plain that meets the ocean in most places along a shallow elevational gradient. A barrier-island system extends the entire length of the southern shore from the town of Southampton on the east to Coney Island within the limits of New York City on the west. Eastward of Southampton, waves have eroded the outwash deposits of the Ronkonkoma Terminal Moraine leaving a "mainland" topography in direct contact with the ocean. The barrier islands are of particular interest because they create large, protected bays between their northern edges and Long Island's south shore. Within these bays, especially from Great South Bay at Captree State Park westward to Jamaica Bay (Fig. 1), extensive salt marshes occur as islands of various sizes and as interrupted fringes projecting into the bays on the northern shores of the barrier islands. Most of Long Island's Seaside Sparrows are found on these southwestern marshes.

The marshes that were surveyed for this study represent both fringing and island types (Fig. 1). *Ammodramus* sparrow populations have been under intensive investigation since the late 1960s at Oak Beach Marsh (OBM) and at West Gilgo Marsh (WGM) (Post 1970a, 1970b; Enders and Post 1971; Post 1974; Post and Greenlaw 1975, 1982). The other marshes reported on here, Captree Marsh East, Cedar Beach Marsh, and Lawrence Marsh, were ground-surveyed for Seasides in July 1981.

SIGNIFICANCE OF PATCHINESS

As noted earlier, Seaside Sparrows are not found everywhere on a Long Island salt marsh. To examine the relationship between the sparrows and marsh microhabitats, I shall first consider their local distributions on the two marshes, Oak Beach Marsh and West Gilgo Marsh, that have been studied most intensively. These marshes contrast with one another in several important respects and together contain all of the major patch-types found in marshes in the region. Then I shall see whether this information permits the prediction of sparrow distributions on selected neighboring marshes that have not been investigated earlier.

Oak Beach Marsh

Oak Beach Marsh is a fringing marsh on the southern edge of Great South Bay about 5 km (3 miles) W of Captree State Park (Fig. 1). Much of the marsh was formed not more than 40 to 50 years ago, so it is relatively low and wet and still contains significant areas of deep pools and tide-influenced mud flat. Except along the bay margin of the marsh, elevations are at or a little above mean high water with the result that tides, mostly storm and high spring tides, only intermittently flood it. Still, elevations are sufficiently gradual and low that water with salinities as high as 26 to 30 parts per thousand tends to stand most of the time on the marsh surface. Ditching has been minimal on OBM and is largely restricted to the northeastern corner and to one large area of salt meadow and adjacent cordgrass in the southwestern section.

MAJOR SALT MARSHES OF SOUTHWESTERN LONG ISLAND

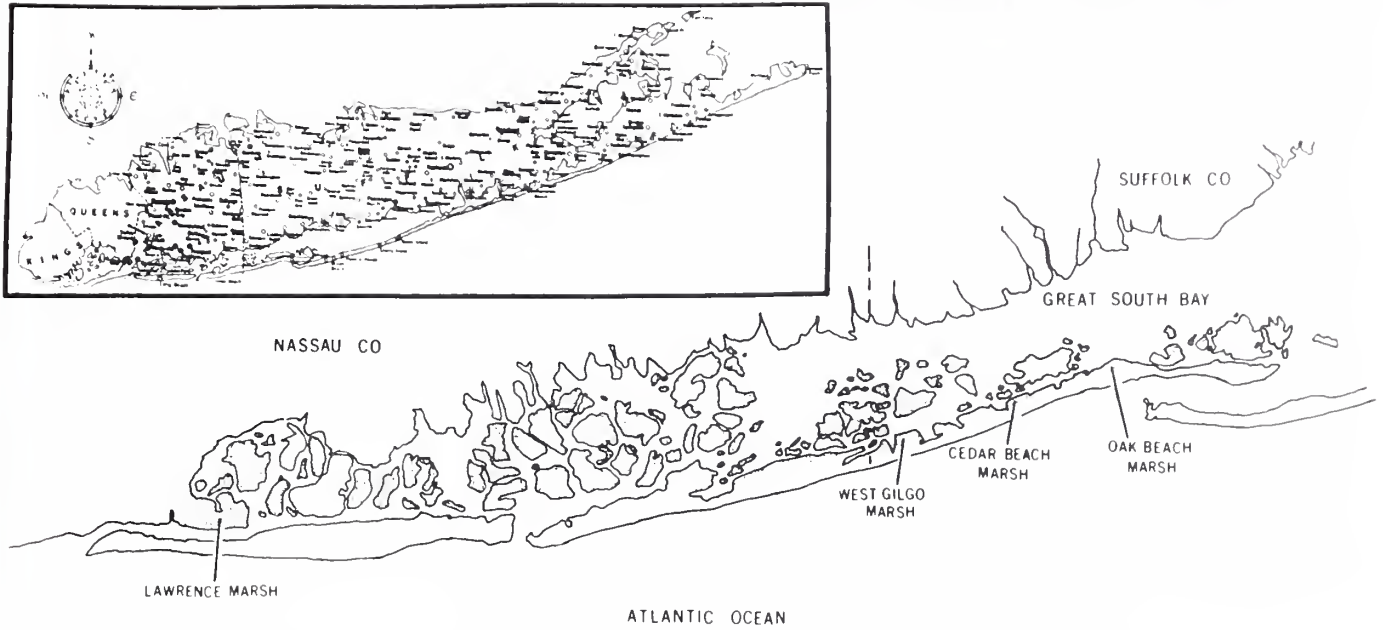


Fig. 1. Major salt marshes (stippled) of southwestern Long Island, New York, and locations of study areas.

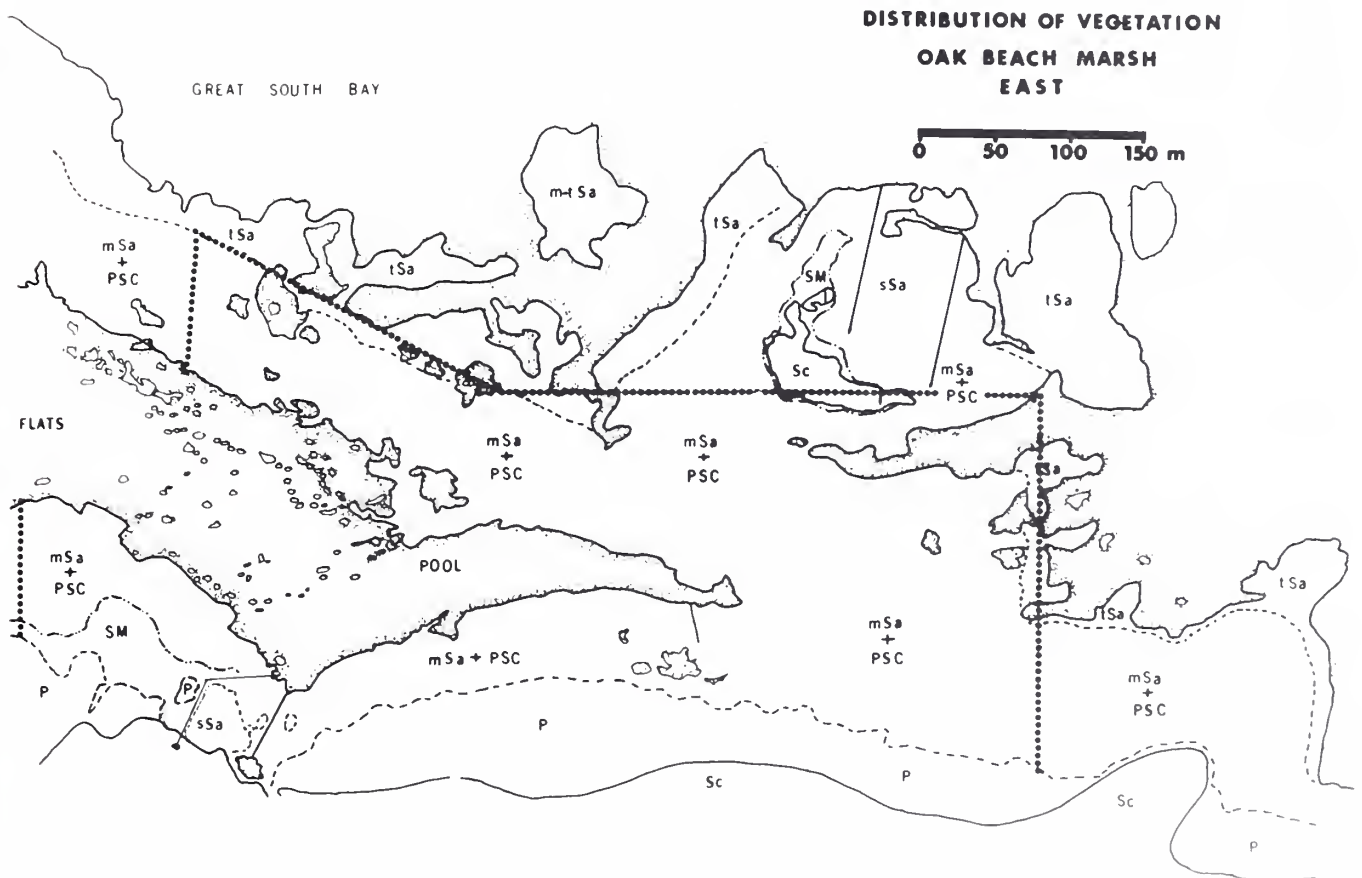


Fig. 2. Distribution of microhabitats on the eastern and central portions of Oak Beach Marsh. The dotted lines enclose the area surveyed for Seaside Sparrows from 1978 to 1980. See key to abbreviations and symbols on page 100.

TABLE 1. Percent of use of microhabitat patches at Oak Beach Marsh and West Gilgo Marsh by foraging Seaside Sparrows in 1977 and 1979.

Locality	No.	Microhabitats ¹						
		MPL	S-MSA	PAN	sSA-SM	SM	I	P
Oak Beach	124	32.2	48.4	16.1	2.4	0	-	0.8
West Gilgo	50	- ²	60.0	-	26.0	4.0	10.0	-

¹ See key to abbreviations and symbols on page 100.

² A dash indicates microhabitats with less than a 5.0% representation in the study area.

TABLE 2. Percent of use of different microhabitats as nest sites by Seaside Sparrows at Oak Beach Marsh and at West Gilgo Marsh, 1977 to 1980.

Locality	No.	Microhabitats ¹					
		SA/PSE	SA/PSC/PSM	W	SA/SM	SM	I/SM
Oak Beach	254	24.0	67.7	5.5	2.8	0	-
West Gilgo	31	- ²	9.7	0	6.4	16.1	58.1

¹ See key to abbreviations and symbols on page 100.

² A dash indicates microhabitats with less than a 5.0% representation in the study area.

The vegetated parts of OBM can be subdivided readily into four major plant communities that differ in floristic composition and in physiognomy. These are (1) salt meadow, (2) Reed Grass (*Phragmites australis*), (3) *Iva* and scrub thicket, and (4) Smooth Cordgrass. The location and extent of these communities on the eastern and central parts of OBM are illustrated in Figure 2, and those on the western section are shown in Figure 10. Salt-meadow, reed, and cordgrass communities are discussed next in relation to their use by Seaside Sparrows. The *Iva*/scrub-thicket community will be treated later under West Gilgo Marsh, where it is more prevalent.

Salt meadow (Fig. 3), consisting primarily of pure stands of *S. patens*, occupies relatively small and well-defined areas on the eastern half of OBM (Fig. 2). But, on the western half, it is more extensive and forms a distinct landward zone of high marsh above mean high water. Where it occurs at OBM its appearance is characteristic. Dead, persistent plants from the previous growing season form a dense, partly flattened, and tufted or "cowlicked" thatch through which the new growth penetrates. Midsummer height of the green grass is about 20 cm, while most of the persistent stems lie within 15 cm of the surface, thoroughly covering the substrate of peaty mud and litter.

Seasides largely avoid unbroken areas of salt meadow of any substantial size (Tables 1 and 2). At OBM, some males incorporated small patches of salt-meadow grass within their territories. They sometimes sang from perches in this patch-type or flew across it to sing from *Phragmites* stems along the adjacent marsh edge. Because foraging Seaside Sparrows favor relatively open spots with access to the mud substrate and to the erect bases of *Spartina* growing there (Woolfenden 1956, Post 1974), they do not find suitable feeding sites in the dense salt meadow. The portions of this plant community used by Seasides at OBM as an occasional nest site or as a feeding site were either near expanses of Smooth

Cordgrass otherwise regularly used or were in cordgrass/salt-meadow ecotones.

Phragmites, or Reed Grass, occurs at OBM primarily as a band of variable width along the landward border of the *Spartina* marsh (Fig. 2 and 4). Thus, Reed Grass separates the marsh proper from the old-dune scrub of the barrier island. It grows as a moderately dense, continuous monoculture reaching 2.5 to 3.0 m in height. Persistent stems generally remain standing over winter and provide cover and singing sites for spring arrivals, and at other times, for males having territories in *Spartina* along the marsh edge. Defended portions of these peripheral territories even include the edge of the adjacent *Phragmites* stand. Seasides often use the open muddy spots and wrack along the margins of the *Phragmites* as feeding sites. Sometimes their foraging beats take them short distances on the litter and mud within the *Phragmites* stands. No nests were placed within this patch-type (Table 2).

Smooth Cordgrass is the dominant grass nearly everywhere at OBM (Fig. 2, Fig. 4 foreground), yet its mere presence is insufficient to explain the local distribution of Seasides using it. As a patch-type, cordgrass can occur in continuous, unbroken stands (Fig. 4) or it can be dissected and interrupted by other microhabitats such as patches of wrack deposited by winter tides, open muddy spots with or without shallow standing water (Fig. 5), deep pools with muddy margins (Fig. 6), and pannes with a sparse growth of Glasswort (*Salicornia* sp.). Seasides commonly occupy territories both in continuous and in discontinuous stands of cordgrass, so their patchy distribution in this vegetation still remains unexplained. The puzzle can be resolved, however, by recognizing several distinctive patch-types within the cordgrass community itself. Marsh microrelief and differential tidal flushing in low marsh and adjacent sections of high marsh are related to the development of two or three ecophenes of *S. alterniflora* defined by average height and tendency to flower (Niering and

Fig. 3. Dense, partly flattened network of stems of salt-meadow grasses (*S. patens* with *I. frutescens* invading) that obscure the underlying substrate of high marsh at Oak Beach Marsh and West Gilgo Marsh.

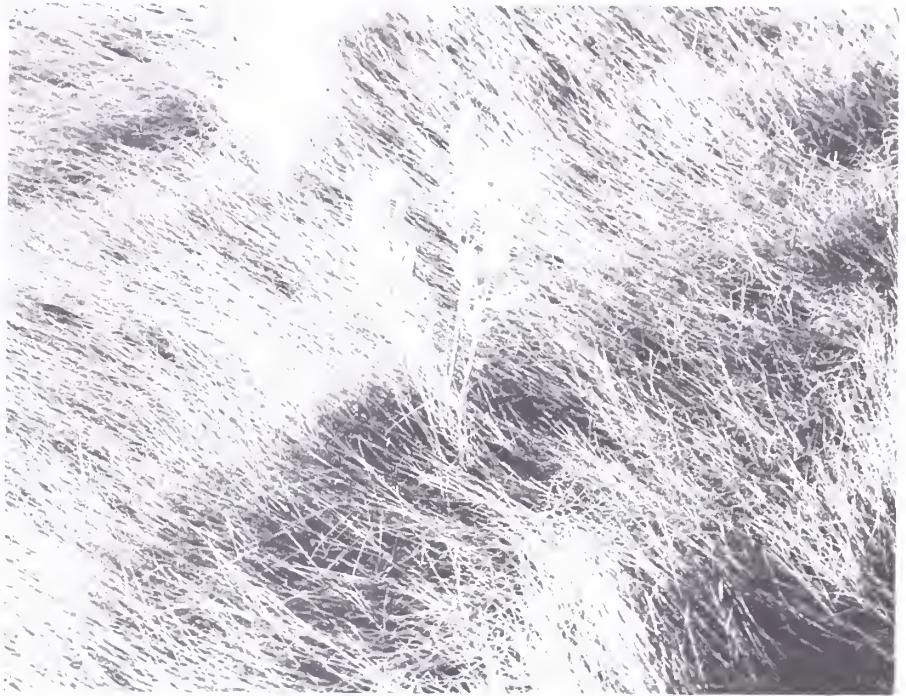


Fig. 4. Midsummer view at Oak Beach Marsh showing erect and clumped *S. alterniflora* of medium height in foreground and the zone of *Phragmites* along its upland edge in the background.



Warren 1980). For present purposes, I distinguish between tall, medium, and short (dwarf) varieties.

The tall form of *S. alterniflora* reaches 1 to 2 m in height and flowers profusely. This ecophene is found at and a little below mean high water along bay and channel margins where regular daily tidal inundations occur. In this patch-type, evenly dispersed and separated live culms, absence of erect persistent stems in dense clumps, regular flooding, and sensitivity to wind damage combine to produce inadequate nesting sites for Seaside. They sometimes feed in the more open spots at low tide in this zone, but generally territories are not located in continuous stands of tall *S. alterniflora* (Fig. 9).

At the other height extreme, the dwarf form spreads vegetatively and may cover extensive areas of marsh in moderately well-drained sites a little above mean high water. In some marshes, it typically forms an ecotone between the salt-meadow marsh (high marsh) and the low marsh occupied by taller varieties of *S. alterniflora*. Culms tend to be evenly dispersed in dense to moderately dense stands (Fig. 5). Here, as in areas of the tall ecophene, Seaside from nearby territories may feed in spots containing openings where access to the substrate and culm bases is possible; but they do not find suitable nesting sites in dwarf *S. alterniflora* and do not establish territories in large, continuous stands of it (Fig. 9 and 10). Small patches of this variety may, however, be

Fig. 5. Muddy panne formed in a stand of dwarf *S. alterniflora* at Oak Beach Marsh.



Fig. 6. A deep pool with muddy margins in a stand of medium-height *S. alterniflora* on the western end of Oak Beach Marsh. The stakes are about 1 m long.



included within the defended space of a male.

Although grass heights of *S. alterniflora* probably constitute a continuum between dwarf and tall forms, it is convenient from the standpoint of Seaside ecology to recognize an intermediate variety of medium height. This ecophene (Fig. 4 and 6) is widespread on OBM (Fig. 2), where it generally reaches 40 to 80 cm in height, occasionally flowers (at least in the wetter sites), and grows densely in many spots, although not as densely as grasses do in the salt-meadow areas. In sites with higher stem densities, winter winds often condense the tops of the longer persistent stems into semi-erect clumps (Fig. 7). Snow cover, heavy winds, and flooding sometimes create patches of matted dead stems parallel

to and elevated above the marsh surface.

In this ecophene of *S. alterniflora*, Seaside appears to favor areas that have a tendency to form dense clumps. These clumps of overwintering grass constitute one of the most conspicuous features on the early-spring salt marsh when sparrows arrive and commence breeding. Such clumps provide suitable elevated nesting sites in May and June before the new growth is tall enough to support nests above water (Table 2). They also are used as singing and lookout perches and as places to seek refuge. Because of varying stem densities locally and the presence of openings, wrack, and muddy pools all around or nearby, this microhabitat contains suitable foraging sites as well (Table 1).



Fig. 7. Clumped, persistent *S. alterniflora* in a stand of the medium-height ecophene at Oak Beach Marsh. These clumps are commonly used as nesting and singing sites by Seaside Sparrows.

Post (1974, p. 569) has pointed out in relation to overwintering *S. alterniflora* that large areas of grass flattened to the substrate or removed by heavy snows, ice floes, and winter flooding tend to be avoided by returning Seasides. Rather, nearby areas of standing vegetation that forms clumps of partly erect stems (even in expanses of otherwise uniformly matted grass) will serve as the foci for newly established territories. It does happen, however, that later arrivals may be able to establish territories in areas with flattened grass when the new growth of *S. alterniflora* pushes up some of the overwintering stems into clumps. Occasionally, Seasides select unusual spots for their nests. For example, they may place them under small pieces of wrack or under areas of matted grass that permit the nests to be elevated above the substrate (Table 2).

The apparent preference of Seasides at OBM for medium-height grasses containing clumped and matted stems is illustrated in Figure 8. Use of this patch-type as nest sites exceeds its percentage of occurrence on the marsh. Medium-height grasses with little or no significant clumping tend to be employed as nest sites only late in the season (July) when the green stems of the current growth are sufficiently dense and tall to be incorporated into the sides of the nest as lateral support and as a canopy over the cup.

By way of summary of the distribution of Seaside Sparrows at OBM, Figure 9 shows the dispersion of "territories" in 1980 on the eastern half of the marsh in relation to microhabitats (compare with Figure 2). Except for differences in sparrow density and in the sizes of the areas surveyed, maps for 1978 and 1979 portray very similar patterns. The sparrows were surveyed in June and early July by systematically visiting every part of the marsh and identifying all birds with the help of a taped primary song to attract them into view. The circled areas on the map represent the centers of defense and singing activities of a resident male. These

areas also contain the nest of the occupant pair and enclose some feeding sites. The boundaries are approximate, however, because individual birds travel varying distances away from the nest in foraging, with the result that overall activity spaces of adjacent males overlap considerably (Post 1974; Greenlaw, unpubl. MS). Results of these surveys suggest that extensive areas of medium-height *S. alterniflora* containing clumped and matted patches of persistent, overwintering plants permit Seasides to settle in high densities with contiguous and overlapping territories. Locally within the population, in spots with numerous mud pools and much clumping of persistent stems, the birds may be quite crowded and the defended spaces very small (for example, around the eastern end of the large pool in Figure 9).

The Seaside Sparrow population also was surveyed in 1977 on the western end of OBM (Fig. 10). This part of the marsh is much more heterogeneous than eastern and central sections, with the result that sparrow dispersion there is patchier. Still, the locations of Seaside territories in the west are entirely predictable from the relations with grass height, density, and clumping discussed above for the eastern birds.

West Gilgo Marsh

West Gilgo Marsh in several respects is more typical of the south-shore marshes of Long Island than is OBM. It is dissected at regular intervals by mosquito ditches, and it contains a larger area of high marsh along its landward edge. Like OBM, which is about 8 km (5 miles) eastward on the same barrier island, it is a fringing marsh jutting into the bay (Fig. 1).

WGM contains all the major patch-types found at OBM, but their respective proportions differ dramatically (compare Figures 2 and 11). The most significant differences between the two marshes were the importance of *Iva* and *Iva*-scrub habitat on WGM and the vir-

tual absence of patches of densely clumped, persistent *S. alterniflora* in its low-marsh sections.

Iva occupies two different parts of WGM: (1) along the landward edge where it mixes with a ground cover of densely growing salt-meadow vegetation and scattered, short *Phragmites*, and (2) on raised areas of old dredge spoil on the marsh. The higher and larger "spoil islands" tend to be vegetated by dense thickets of *Rhus*, *Prunus*, and *Myrica*. Song Sparrows (*Melospiza melodia*) favor these sites, but Seaside Sparrows use them only as song posts or sources of refuge. The lower "spoil islands" (Fig. 12) are covered with *Iva* about 1.0 to 1.5 m high and salt-meadow grasses that tend to form clumps around the bases of the *Iva*. Wrack sometimes collects in patches along the edges of these islands.

Seaside Sparrows mostly nest on the *Iva* islands (Table 2) where flooding presents a minimal problem and cover is abundant. They usually place their nests above ground in the taller clumps of grass at the bases of *Iva*. One nest, however, was near the top of an *Iva* plant 62 cm above the substrate, and several others were in *Iva* nearer the ground. The sparrows also feed in these *Iva* habitats and the associated patches of wrack (Post 1974, Table 2); but much of their foraging also occurs in the diverse patch-types immediately around the spoil islands or nearby. Favored microhabitats used for this purpose are areas of short, open *S. alterniflora*, medium-height *S. alterniflora* of low to moderate density, *S. alterniflora*/salt-meadow ecotones with openings, ditch edges, and pool margins. Woolfenden (1956, 1968), who studied a New Jersey population occupying a similar marsh, found individual Seaside Sparrows that flew about 90 m across unsuitable habitat to feed along the marsh edges nearest their nests.

The *Iva*-centered territories of Seaside Sparrows at WGM are several times larger than those at OBM (Post 1974, pers. obs.), and because of the small size and patchy distribution of the spoil islands, they are irregularly distributed and tend to be overdispersed with only one or two contiguous neighbors at most. One pair was isolated on a small patch of *Iva* only 3 to 4 m across, about 50 m from its nearest neighbors.

As on OBM, Seaside Sparrows on WGM seemed to avoid the large, continuous areas of salt meadow. Only two pairs in 1981 (Fig. 11) had a nest in the landward zone of *Iva* and salt meadow, but in this case the pure salt-meadow zone nearby on the marsh was interrupted by large patches of short *S. alterniflora*, *S. alterniflora*/salt-meadow ecotone, and ditch edge that provided contiguous feeding sites.

The large area of low marsh occupying the outer two-thirds of WGM highlights the primary importance of persistent grass clumping as a focus for Seaside Sparrows in medium-height *S. alterniflora*. Winter snows of 1977-1978 completely flattened the persistent grass to water level everywhere in this part of the marsh. Although some Seaside Sparrows evidently found suitable nesting conditions in this low-marsh area in the early 1970s (W. Post, pers. comm.), no birds nested there in the summers of 1978 to 1980. Grass in this part of the marsh, although of medium height, was somewhat open and exhibited little clumping (Fig. 13). In 1981, one small area in the central-eastern part of the outer marsh had a high density of medium-height persistent *S.*

alterniflora that exhibited distinctive clumping. One pair of Seaside Sparrows occupied this spot. The birds were isolated from their nearest neighbors on *Iva* islands (Fig. 11).

In summary, Seaside Sparrows find suitable feeding and nesting conditions at OBM and WGM on both low-marsh and high-marsh sites (Fig. 14). Small and often contiguous, low-marsh territories are confined to areas of *S. alterniflora*, which offer clumps of persistent grass that permit the birds to build protected nests above normal tidal fluctuations. Foraging is possible immediately around the nests. High-marsh territories are larger and usually dispersed because they are centered on irregularly distributed patches of *Iva*. Feeding sites tend to be nearby but separated from the *Iva* where the birds nest. Occasionally birds travel 100 m or more to a foraging site (Post 1974).

THE SITUATION ON OTHER MARSHES: PREDICTION OF LOCAL DISTRIBUTION

Using aerial photographs, I mapped the microhabitats of several other marshes along the southwestern Long Island shore and subsequently surveyed them for Seaside Sparrows. One of the marshes (Captree Marsh East) appeared to have limited feeding and nesting sites within radii of 100 m or less. Spoil islands covered with *Iva* and areas of medium-height grass containing clumps of persistent stems were absent. Judging from the patterns observed at OBM and WGM, Seaside Sparrows should be absent also. Indeed, two surveyors failed to locate breeding Seaside Sparrows on this marsh. Two other marshes, Cedar Beach Marsh and Lawrence Marsh (Fig. 1), contained vegetation types similar to those described above, but each was different in several respects from all the others visited. I judged that sparrows would be present on the two marshes and that their location on each marsh would be unique and predictable.

Cedar Beach Marsh

Cedar Beach Marsh (CBM) is another fringing marsh on Great South Bay about 2 km (1.2 mile) W of OBM. It is a relatively narrow marsh, but it contains the distinctive inner zone of salt meadow and an outer low marsh. Ditching is mainly confined to the eastern and seaward sections. Aerial photographs show that the major patch-types on the eastern two-thirds of this marsh consist primarily of salt-meadow grasses, shorter varieties of Smooth Cordgrass, and two spoil islands covered with a dense growth of dune scrub. None of these patches at OBM and WGM (above) offers both suitable nesting and feeding sites within reasonable commuting distance, so it was expected that Seaside Sparrows would be absent from this part of CBM as well. An area of medium-height *S. alterniflora* with clumped grasses occurs in a slight depression in the central portion of the marsh around a large pool and several smaller pools between the salt-meadow zone and a large area of dune scrub towards the bay. This area should contain a small population of Seaside Sparrows.

We ground-surveyed this marsh in mid-July (Fig. 15). Seaside Sparrows indeed were absent from most of the marsh where we did not expect to find them. The only exception was a single territory-sized patch of medium-height live and clumped persistent grasses (not

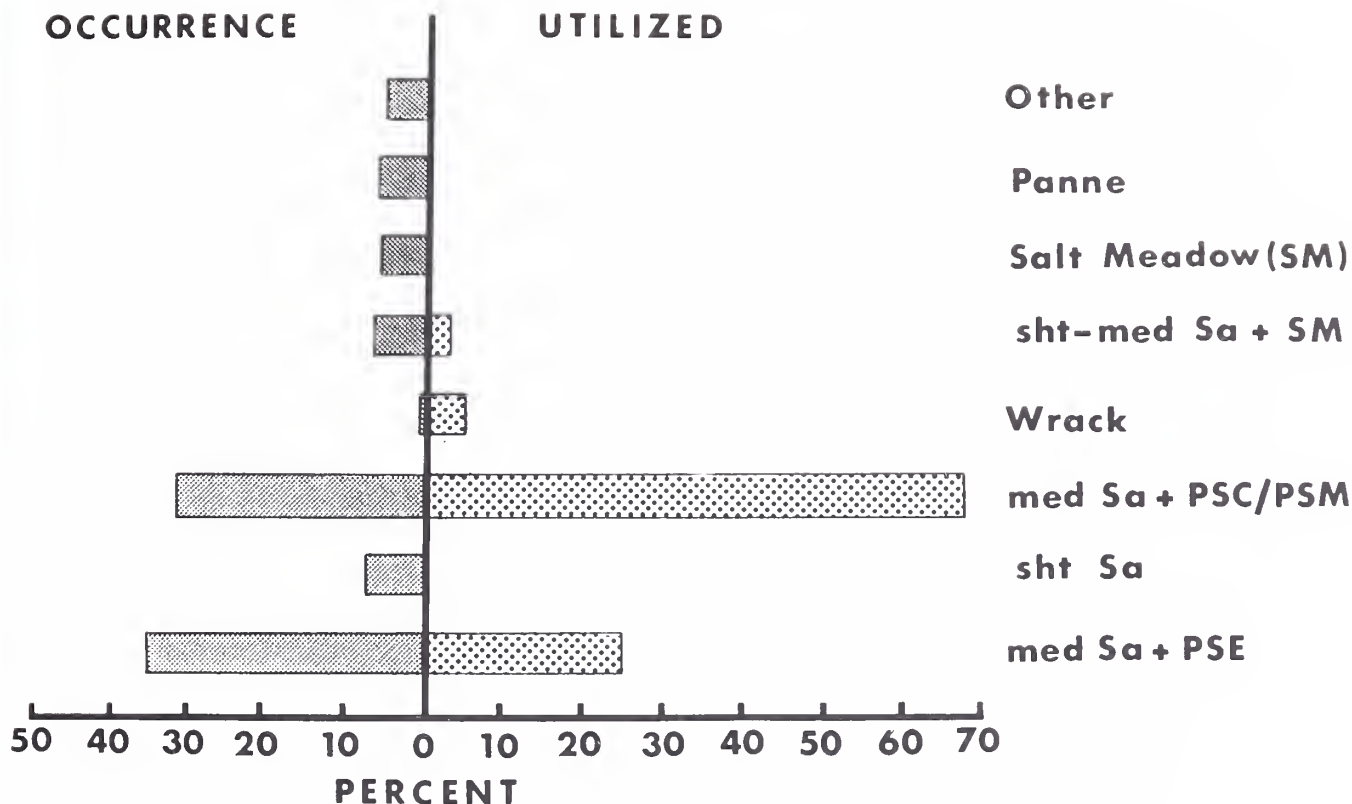


Fig. 8. Use of different vegetation patches as nesting sites by Seaside Sparrows in comparison to their occurrence in random samples (point-centered quadrats, Wiens 1969; $n = 415$) at Oak Beach Marsh. See key to abbreviations and symbols on page 100.

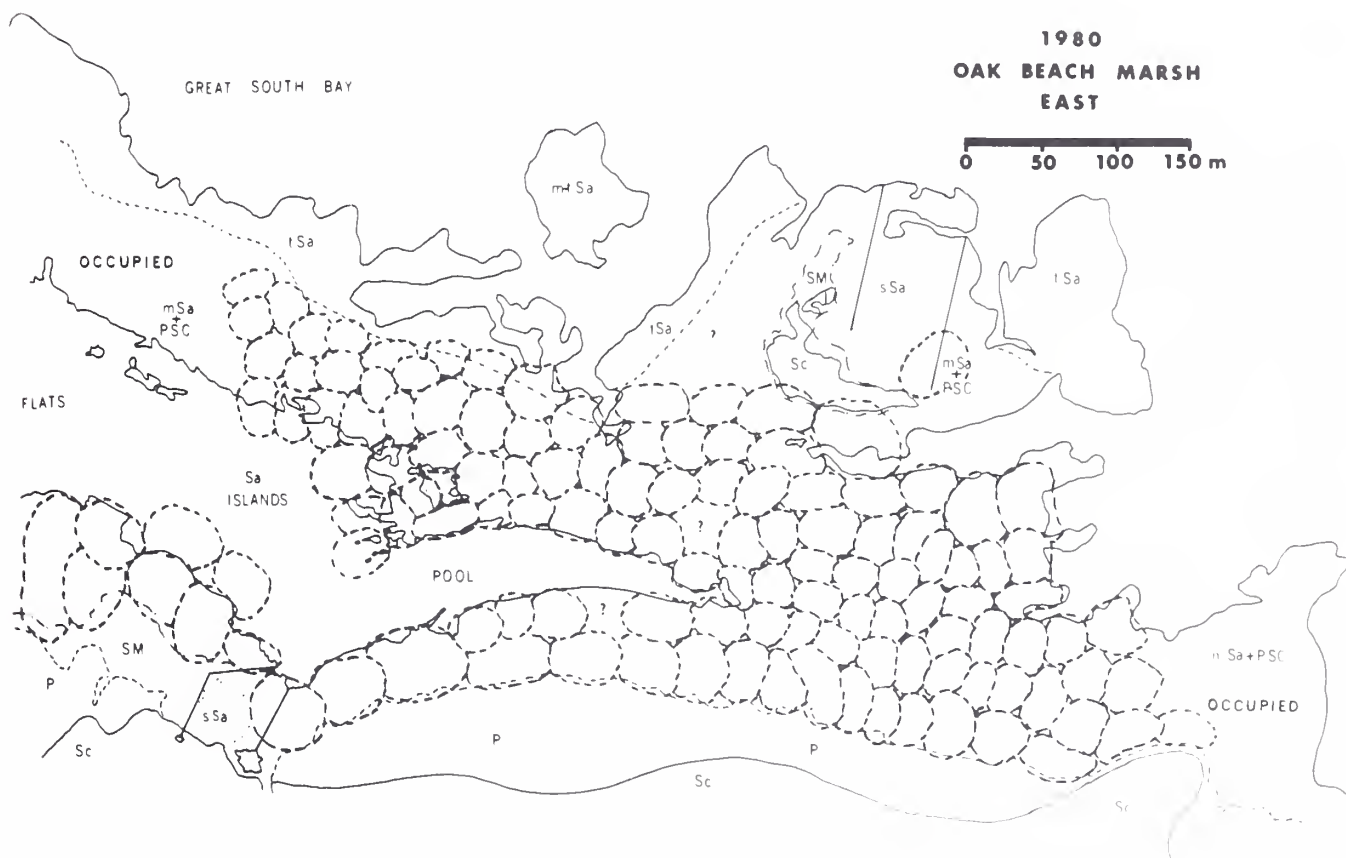


Fig. 9. Distribution of Seaside Sparrows at Oak Beach Marsh in 1980 in relation to microhabitats on the marsh. Dashed lines represent approximate boundaries enclosing defended and singing areas of resident males. See key to abbreviations and symbols on page 100.

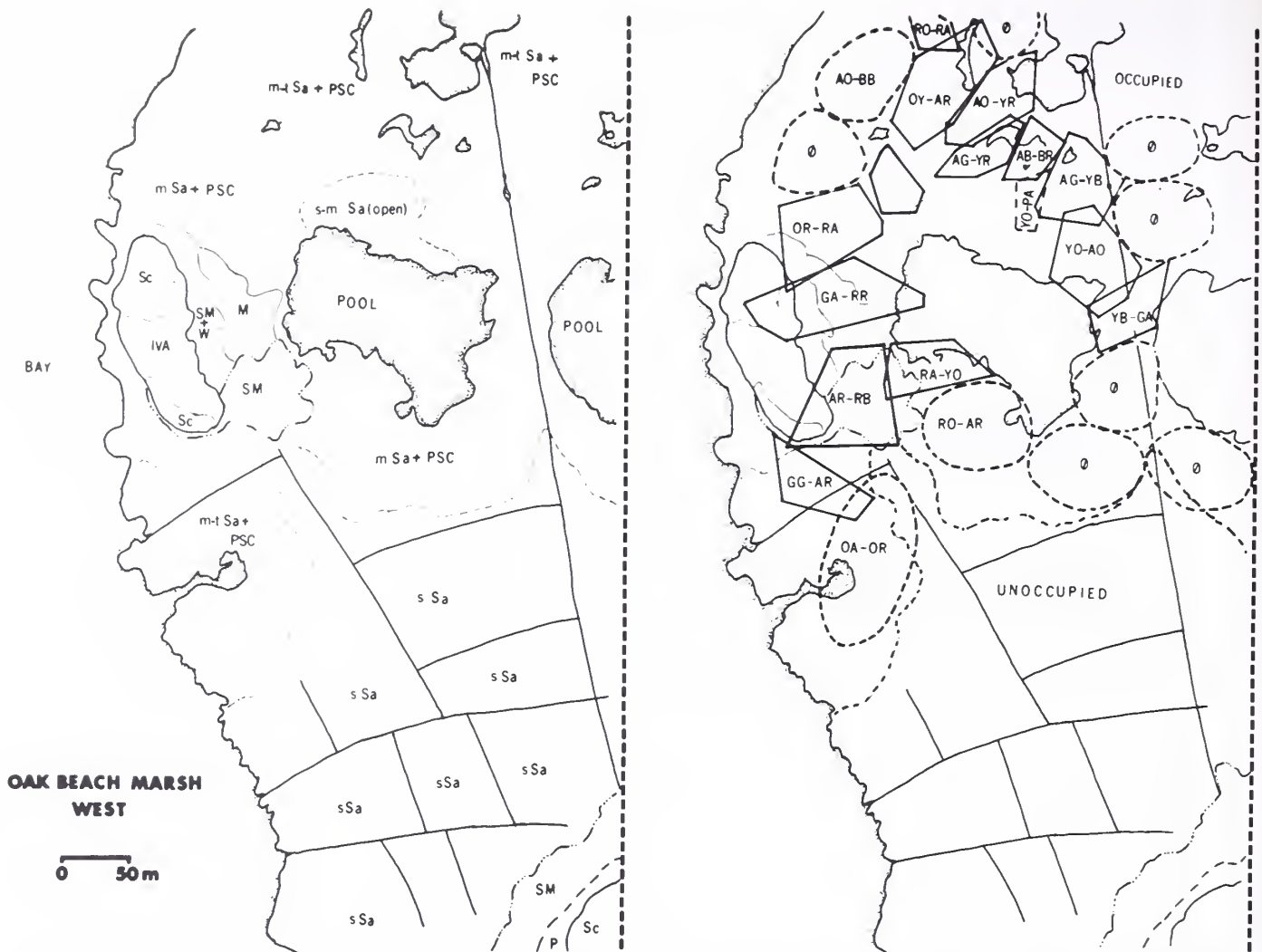


Fig. 10. Cover map showing microhabitats (left) and distribution of Seaside Sparrows in relation to these microhabitats (right) on the western end of Oak Beach Marsh in 1977. Solid lines delimit maximum-sized polygons containing all observed song and defense sites used by resident males. See key to abbreviations and symbols on page 100.

visible in the aerial photographs available) growing in the east-central section. One pair of Seasides resided here isolated from their nearest neighbors to the west. In the larger patch of medium-height and clumped *S. alterniflora* in the central part of the marsh around the pools, we found—as expected—a group of about 12 to 15 small, contiguous territories. These birds foraged around the pool, in more open patches of grass within their territories, in neighboring short-grass *S. alterniflora* providing access to the substrate, and probably along the bay as well.

Thus, the local distribution of Seasides at CBM was predictable based on observed patterns at OBM. No high-marsh territories were expected or found.

Lawrence Marsh

Lawrence Marsh occupies a broad peninsula connected to the mainland near the western end of the bay/barrier-island complex in Nassau County. It is separated from Atlantic Beach and Long Beach on the neighboring barrier island by a boat channel. We surveyed the eastern half of this marsh in mid-July on foot and by boat.

Away from the channel margins, this marsh is extensively covered by shorter ecophenes of *S. alterniflora*.

flora. Taller grass occurs in narrow bands along the larger channels. There are remains of old ditches on the marsh, but evidently they are not maintained.

The occurrence and distribution of the different patch-types on Lawrence Marsh (Fig. 16) suggested that Seaside Sparrows would be restricted to an area relatively free of ditches and to the edge of the boat channel where *Iva*-covered spoil islands are found. Thus, this marsh should include Seaside populations with dispersions characteristic of those on OBM and WGM. Other parts of the marsh should be unoccupied.

On the eastern part of Lawrence Marsh, we failed to find Seasides in the areas of shorter *S. alterniflora* covering most of the marsh. But, as expected, birds were on small, contiguous territories in the large patch of low marsh containing medium-height *S. alterniflora* and clumps of persistent grass. This part of the marsh occupied a slight, shallow depression that was somewhat wetter than neighboring short-grass (and ditched) areas all around (Fig. 16). Also present were numerous large pools with broad muddy margins that were used by sparrows as foraging sites. The situation here resembled that at OBM.

Two groups of small spoil islands covered by *Iva* and salt-meadow grasses also were occupied by Sea-

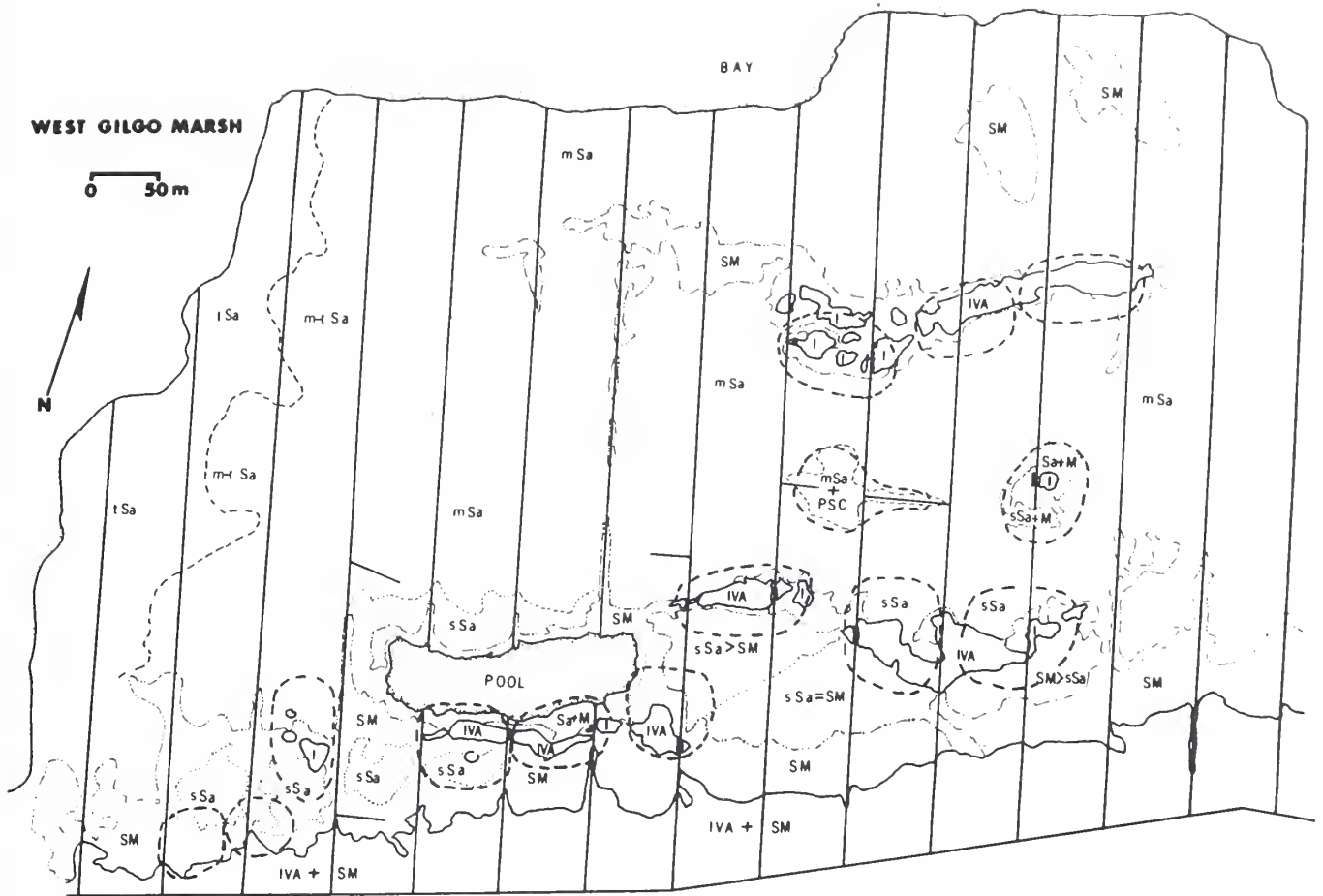


Fig. 11. Microhabitats and distribution of Seaside Sparrows in relation to them at West Gilgo Marsh in 1981. See key to abbreviations and symbols on page 100.

sides, corresponding to the pattern at WGM. One group of islands was about 50 to 70 m from the low-marsh population in a part of the marsh otherwise covered by short *S. alterniflora*. The behavior of two pairs suggested that active nests were in the *Iva* patches. The open grass of the stands of short *S. alterniflora*, the small pannes, and the large mud pools associated with the nearby low marsh probably provided suitable feeding sites within easy commuting distance. An *Iva* island used by one pair consisted of only a few shrubs and a small patch of salt meadow surrounded and isolated by extensive mud flat and pools. However, a large *Iva* island and one covered by dense scrub over 100 m from the flats and mud pools were not occupied. Perhaps the large distance separating a potential nest site from potential foraging sites prevented their use.

Finally, a second group of *Iva*-covered spoil islands occurred near the edge of the boat channel (Fig. 16). Here again, territories centered on these "islands" occurred in a loose, overdispersed pattern. Muddy areas and wrack in the intertidal zone nearby along the channel provided convenient foraging opportunities.

DISCUSSION

Habitat Selection by Seaside Sparrows

Recent studies of ecological distribution in birds have stressed the importance of habitat structure in understanding patterns of occurrence in relation to

plant communities (MacArthur and MacArthur 1961, Wiens 1969, James 1971, Anderson and Shugart 1974). Many such studies have been content, however, to identify habitat variables that simply correlate with the presence of a bird species. In my case, using a nonstatistical technique in a simple but patchy environment, I am able to identify biologically significant structural features of salt-marsh environments on Long Island that distinguish clearly habitat where Seaside Sparrows are present or absent.

At least in broad terms, it seems possible to generalize on the patterns of habitat use observed in Long Island Seaside breeding populations. But, in doing so it is important to recognize that the species' microgeographic distribution in relation to salt-marsh heterogeneity can be understood and evaluated only as functions of the dominant activities that the birds perform in carrying out a successful reproductive cycle. These activities are all nest-related or nest-centered and include collecting nest material, siting nests, caring for young, singing, and feeding. Nests are situated in such a way that they are in or near favored feeding areas, have suitable cover and support, and are sufficiently elevated to reduce the danger of flooding. Singing and visual inspection of defended areas require relatively stiff, raised perches. Generally, the clumps of grasses and *Iva* that offer nest sites also are used as song and lookout posts. In addition, any other elevated object or plant in a male's activity space may be employed as

Fig. 12. Small "islands" of *Iva* surrounded by patches of salt meadow and short *S. alterniflora* (foreground) at West Gilgo Marsh. Seasides nest in patches of open *Iva* and salt meadow and feed nearby in open cordgrass.



Fig. 13. Expanse of *S. alterniflora* characterized by evenly spaced stems (no clumping) of medium height on the outer portion of West Gilgo Marsh. Seasides have not occupied this area in recent years, at least since the grasses on the area were flattened by winter snows in 1977-1978.



opportunity arises. This important behavior then seems to have habitat dependencies that are functions of nest sites or are otherwise commonly met in suitable breeding areas. The same appears to be true of other activities as well. Thus, the habitat features that are associated with the different requirements of the dominant behaviors of feeding and siting nests seem to be sufficient for predicting the Seaside's local breeding distribution on Long Island salt marshes. In effect, the bird's "niche-gestalt" (James 1971) is represented as in Figure 14 by segments of a salt-marsh profile that contain biologically significant patch-types within reasonable commuting distances.

Yet, in addition to its general relations with patch-types, one also should stress that Seaside Sparrows, within limits, are quite opportunistic about using the almost endless variation in detail of patch-type dispersions on different Long Island marshes. The vegetation of high marshes is quite different from that of low marshes, yet locally both provide suitable breeding habitat for the species. Evidently the Seaside's abilities to scale its life-history variables (e.g. territory size, commuting distance, feeding behavior) in relation to local circumstances is sufficiently well developed that at least some aspects of reproductive success are the same in both high-marsh and low-marsh areas (Post 1974;

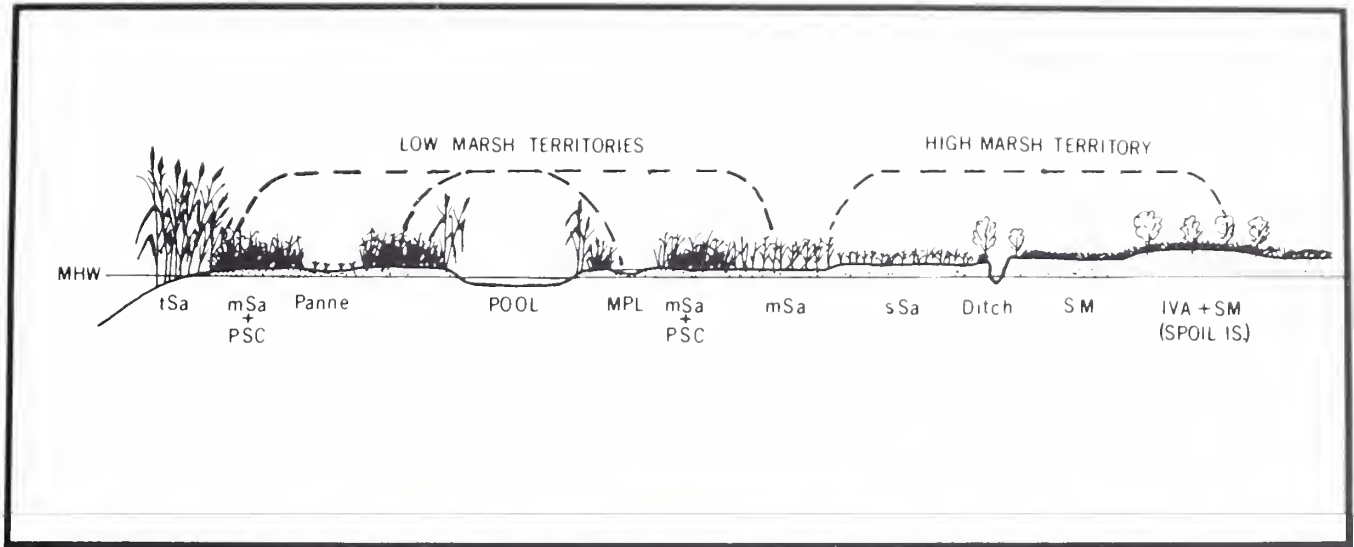


Fig. 14. An idealized profile of a Long Island salt marsh summarizing the general relationships between microhabitats that can occur there and the locations of Seaside Sparrow territories. Overlapping low-marsh territories should be relatively small compared to high-marsh territories. See key to abbreviations and symbols (page 100) for all such terms except MHW (mean high water).

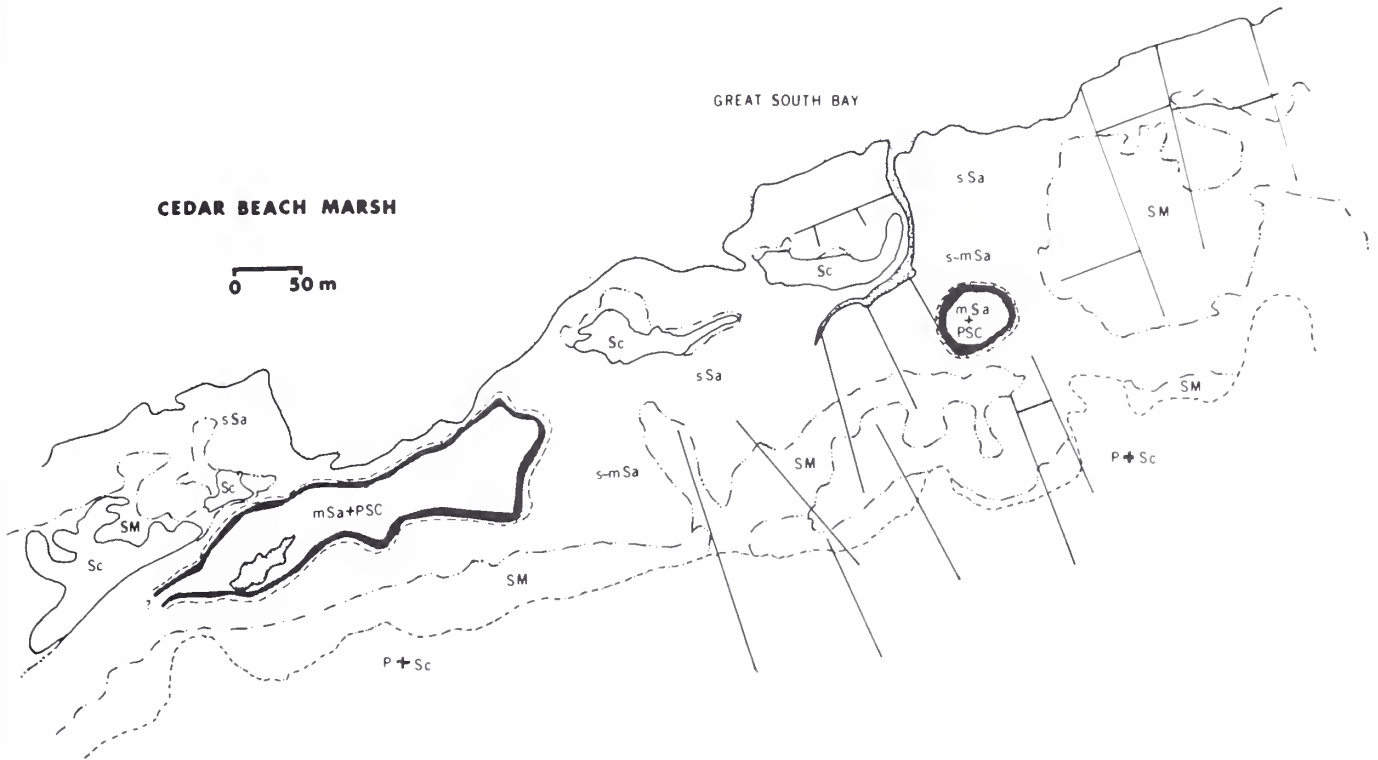


Fig. 15. Relationship between the occurrence of Seaside Sparrows (enclosed by shaded lines) and microhabitats on Cedar Beach Marsh in 1981. The small area on the right was occupied by a single, isolated pair. The larger area on the left contained a population of 12 to 15 males. See key (page 100) for explanation of abbreviations.

Greenlaw et al., in prep.).

In certain southern marshes, interspecific interaction with the Rice Rat (*Oryzomys palustris*), a nonavian competitor for nest sites, evidently plays an important role in determining the ecological distribution of breeding Seaside Sparrows (Post 1981). On Long Island, the only potential competitor is its congeneric relative, the Sharp-tailed Sparrow. The Seaside is aggressively dominant over the Sharp-tailed Sparrow, but we have no

evidence that either species' use of coinhabited marshes is limited in any significant way by the activities of the other (Greenlaw and Post, unpubl. MS).

Habitat Use in Other Parts of Its Range

The question arises whether the patterns of habitat choice observed on Long Island also apply in other parts of the range of Seaside Sparrows. Populations occur discontinuously from Massachusetts to the southern Gulf

Coast of Texas. In most of its range, the species is restricted to salt marshes, but two populations in Florida (*A. m. nigrescens*, now effectively extirpated, and especially *A. m. mirabilis*) also occupy freshwater marshes.

In the Northeast, published information on habitat use in Seasides is available for only one other population, that in Ocean County, New Jersey, where Woolfenden (1956) did his seminal work on *Ammospiza* sparrows. In his population, Seasides occupied a ditched marsh where they nested in patches of *Iva* and associated salt meadow (*Juncus gerardi*) and traveled to nearby feeding areas along the bay shore. The dispersion of the territories and the birds' use of patch-types generally correspond to patterns observed at WGM on Long Island. Similar relations may prevail in Seaside populations in Rhode Island marshes (F. C. Golet and S. E. Reinert, pers. comm.). Thus, populations referable to the race *A. m. maritima* occur in similar marshes and all may show similar patterns of habitat use.

Information on the ecological distribution of Seasides in the mid-Atlantic populations (*A. m. macgillivraii* and *pelonota*) is sparse but suggestive. Where they occur, the birds generally are associated with protected salt marshes behind barrier islands. They may also use brackish marshes back from the coast (Sprunt and Chamberlain 1970). As in the northeast, they exhibit a patchy distribution on the marshes and often occupy areas of Smooth Cordgrass (Tomkins 1941, Nicholson 1946). Tomkins (1941) in particular emphasizes the importance to Seasides of suitable elevated nesting cover and open feeding sites that are commonly separated on salt marshes but within easy flying distance. As expected, the birds show some plasticity in using occupied communities. They place nests most often in dense clumps of grasses or sedges (*Spartina*, *Distichlis*, *Juncus*, *Sporobolus*) and occasionally in shrubs and small trees, such as *Baccharis* and mangroves (*Avicennia*), that are near feeding areas. These are all patterns that are repeated by Seasides on Long Island marshes.

The only other populations of Seaside Sparrows that are well-known ecologically are those in peninsular Florida (*A. m. nigrescens*, *mirabilis*, and *peninsulae* in particular) (Post 1981; Post et al., this symposium; Nicholson 1928; Sharp 1969 and 1970; Trost 1968; Werner 1975). Nicholson (1928) describes the patchy nature of *A. m. nigrescens* habitat, its use of grass clumps and suitable shrubs as nest sites and of open muddy spots as feeding sites, and its tendency to commute between separate feeding and nesting areas. Evidently in some places *A. m. nigrescens* also occupied marshy areas with considerable brush, but when woody vegetation became dominant, the bird disappeared (Sharp 1969).

Werner (1975) performed detailed habitat analyses in *Spartina*, *Cladium*, and *Muhlenbergia* communities occupied by breeding *A. m. mirabilis* in south Florida. This race appears to be unique within the species in having a habitat response that is dependent on the occurrence of periodic fires. The communities occupied by *A. m. mirabilis* exhibit a fairly wide range of physiognomic features including percentage of dead and live biomass, graminoid height, forb height, and plant species richness. Yet, birds in this population evidently favor habitats with certain predictable features that

again are probably related to nest site, feeding, and song-perch requirements. These features are quite similar to those reported in other Seaside populations. Optimal *mirabilis* habitat may be characterized as moderately dense grass-dominated, seasonally wet prairies with vegetation occurring in a clumped or otherwise patchy dispersion pattern, with forbs present and mixed with grasses of intermediate height (up to about 1 m), and with significant proportions of dead, persistent stems that provide suitable nest-sites and cover (Werner 1975, p. 87 and 91). Access to the ground also is important. In dense vegetation the dead material apparently accumulates over a period of a few years, and the site becomes unsuitable to Seaside Sparrows.

Finally, habitat use by *A. m. peninsulae* appears to correspond in general to the patterns outlined above for other populations (Post et al., this symposium). As noted earlier, however, interference competition from the aggressively dominant Rice Rat may modify the Seaside's response to patch-types as nest sites (Post 1981).

There appears to be a specieswide pattern of Seaside habitat use that requires for optimal habitat the presence of (1) suitable elevated nest sites that offer protection from predators and flooding and (2) openings at ground level that permit movement on relatively uncluttered ground and easy access to the bases of surrounding plants. In salt marshes the patch-types that exhibit the appropriate physiognomic features meeting these requirements are often distributed in a mosaic and separated from one another. Thus a third requirement appears to be a relative contiguity of nesting and feeding areas that minimizes commuting time and energy. Structural features of habitat generally associated with such patches are spatial heterogeneity in plant density, clumping of grasses, presence of dead stems, and vegetation of at least medium height. As a rule these patch types occupy an intermediate position along a water gradient in salt marshes.

'Coloniality' in Seaside Sparrows

Patchy, uneven dispersion is so characteristic of the structure of Seaside Sparrow populations that most students of the species have commented on it. Tomkins (1941, p. 46-48) specifically argues that Seasides are semicolonial. This argument is partly dependent on the observation that seemingly suitable habitat goes unused on the South Carolina and Georgia salt marshes where he observed the birds. Others also have employed the term "colony" or "colonial" to describe the local distribution of Seaside populations (e.g. Nicholson 1928 and 1946, Stimson 1968, Werner 1975).

Post (1974) was the first to provide evidence that clumping in Seaside Sparrow populations results from nest-site selection in patchy environments. This patchiness may be readily detected early in the breeding cycle but becomes obscured later when the new crop of grass is tall and of uniform height. This map study of the ecological distribution of Seasides confirms Post's work: The birds appear to respond to specific features of habitat structure, occupying all suitable areas and avoiding patches where these features are absent. Large patches contain large populations with contiguous and overlapping territories. Very small, isolated patches may contain only a single, isolated pair. In some marshes

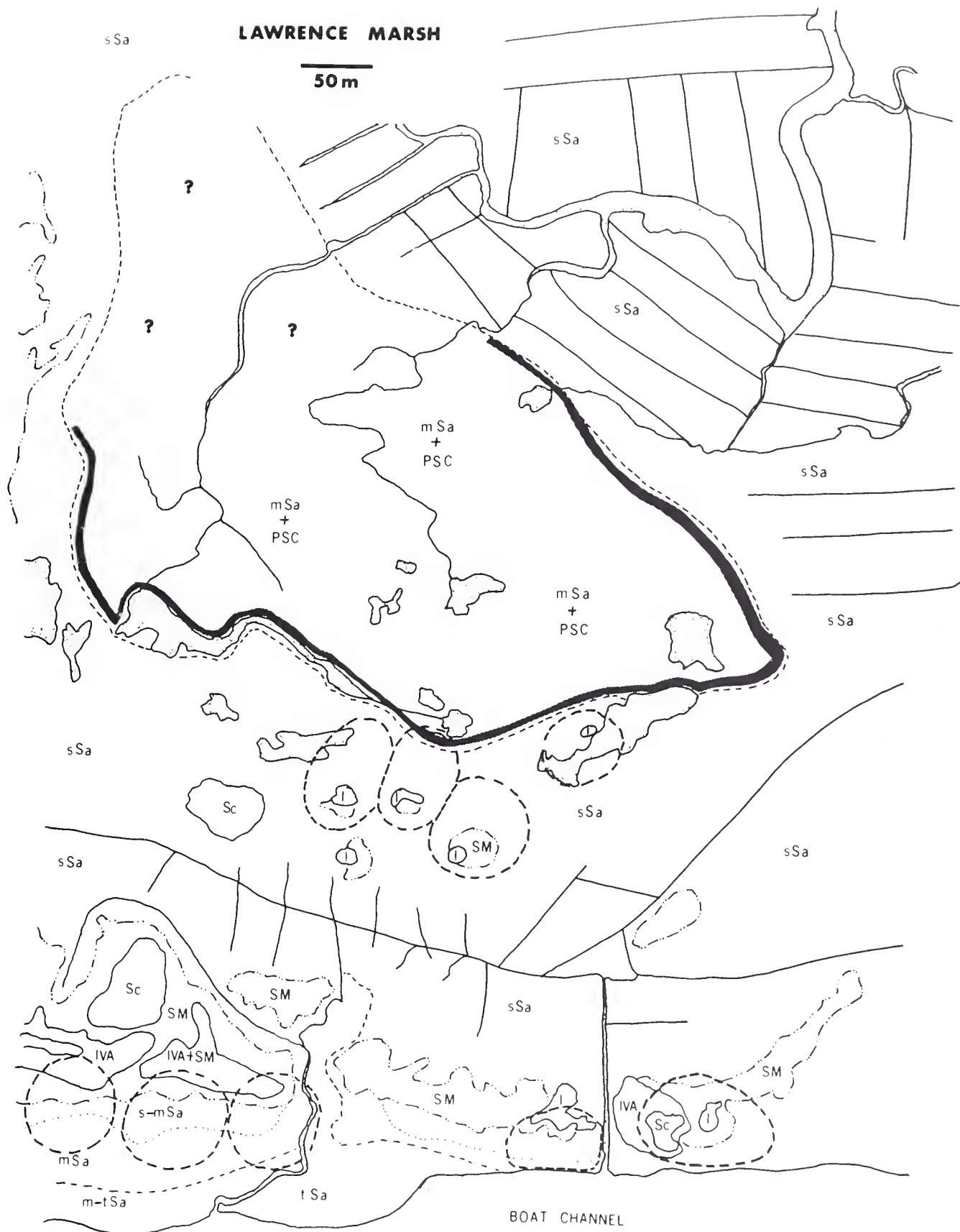


Fig. 16. Relationship between the occurrence of Seaside Sparrows and microhabitats on Lawrence Marsh in 1981. The area enclosed by the shaded line contained a large population of sparrows. The queried section was not ground-surveyed but probably also contained additional Seasides. Approximate boundaries of individual sparrow territories centered on *Iva* patches are shown by the heavy dashed lines. Abbreviations are explained in the key on page 100.

the response of the sparrows to marsh heterogeneity may be modified by competition with other species for nest sites (Post 1981). Thus, we provide no support for the assertion that Seaside Sparrows are "colonial" in any true sense of social affiliation. Rather, the clusters of sparrows are best viewed as "aggregations" until evidence to the contrary is forthcoming (see also Post et al., this symposium).

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Food Habits of Nestling Seaside Sparrows in Unaltered and Ditched Salt Marshes on Long Island, New York

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Abstract. The food habits of nestling Seaside Sparrows in an unaltered salt marsh at Oak Beach and a ditched salt marsh at West Gilgo, New York, were studied during 1978. Dietary samples were collected from nestling sparrows using the neck-collar technique. Nestling Seaside Sparrows at both study sites consumed a wide variety of invertebrates. At Oak Beach, the most frequently eaten foods were adult and larval Stratiomyidae, adult Ephydriidae, and Miridae, whereas at West Gilgo the nestlings' most frequently eaten foods were Araneida and immature and adult Tabanidae. Indices of prey diversity were similar between the nestlings at the two salt marshes. Most of the food items collected from nestling Seaside Sparrows at both salt marshes were altered prior to feeding, and were recovered in the form of a mucous-bound bolus. At Oak Beach, the frequency of smaller-sized foods (<0.01 cc) in the diet of nestling Seaside Sparrows decreased as the frequency of larger-sized foods (>0.05 cc) in their diet increased with age. In contrast, at West Gilgo there were no apparent trends in the sizes of food items fed to nestlings as they grew older. The total volume of food delivered to nestling Seaside Sparrows at Oak Beach increased significantly as the nestling grew older, but at West Gilgo the volume of food fed to nestlings did not increase as they grew older. The foods delivered to nestling Seaside Sparrows indicate that parent Seaside Sparrows at Oak Beach take a significantly higher proportion of their food from the vegetation than do parent Seaside Sparrows at West Gilgo, where they delivered nearly equal amounts of food to their nestlings from the ground and vegetation column.

The Seaside Sparrow (*Ammospiza maritima*) is a common breeding bird in many salt marshes along the Gulf Coast and the Atlantic Coast, north to Massachusetts. Although much is known about the biology and ecology of Seaside Sparrows, information is limited on their specific food habits. Judd (1901) examined the stomach contents of 30 Seaside Sparrows, and reported that their diet was similar to that of the Sharp-tailed Sparrow (*A. caudacuta*), which ate 81% animal matter and 19% vegetable matter. Judd's conclusion that the Seaside Sparrow is highly insectivorous was confirmed by the observations of Woolfenden (1956) and Elliot (1962). Post (1974) compared the types of food items brought to nestling Seaside Sparrows in unaltered (natural) and altered (ditched) salt marshes, but not in much detail. Merriam (1979) provided a more detailed

description of the diet of nestling Seaside Sparrows, but only in an unaltered salt marsh. The purpose of this paper is to describe the food habits of nestling Seaside Sparrows in unaltered and ditched salt marshes.

MATERIALS AND METHODS

I conducted this study during June, July, and August 1978 on two salt marshes on the southern shore of Great South Bay, New York. The first study area at Oak Beach is an unaltered (natural) salt marsh, which has not been extensively ditched for mosquito control purposes. The marsh is 125 to 250 m wide. Normal tidal fluctuations have little effect on the level of standing water on the marsh; only when spring tides combine with north winds is the entire marsh flooded. The standing vegetation (Table 1) consists mainly of *Spartina alterniflora* Loisel., which averages 50 to 100 cm in height and can reach 160 cm along the edge of the bay. There are several large permanent pools that support Widgeon Grass (*Ruppia maritima* L.) and green algae

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(*Cladophora* sp.). Shallow, muddy depressions generally contain water except during very dry periods. Mucky pannes containing Glasswort (*Salicornia europaea* L.) and a sparse growth of dwarf *Spartina alterniflora* are found in sections of marsh (16.6%) toward the bay. The landward side of the marsh supports a dense stand of *Phragmites communis* Trin. (most not included in calculations of percent of cover) and small patches of salt-meadow grasses, *S. patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene.

The second study area is 9 km W of Oak Beach at West Gilgo. This salt marsh is transected by a number of ditches about 25 m apart. The ditches were constructed during the 1930s (Taylor 1938) for mosquito control and are maintained by the Nassau County Mosquito Control Commission. The percent of cover for various plants at West Gilgo is much different than at Oak Beach (Table 1). The salt-meadow grasses cover most of the study area at West Gilgo (50.5%), especially the higher marsh sites. There are fewer mud pools and stands of *S. alterniflora* at West Gilgo than at Oak Beach. There are a number of spoil islands on the marsh at West Gilgo (a result of ditch maintenance operations), which support *P. communis* and *Iva frutescens* L.

Several studies have been conducted in these marshes, and additional descriptions of the areas can be found in reports by Post and Enders (1970) and Post (1970, 1974).

In April 1978 the study sites were surveyed and gridded using labeled stakes (1-m furring strips) at 25-m intervals. I used wire prongs on the top of the stakes to discourage their use by predatory birds. At Oak Beach, I mapped the different zones of vegetation and terrain features, and calculated the percent of cover for each patch type by using a compensating polar planimeter. At West Gilgo, I determined the percent of cover for the various patch types by taking transects of the marsh from the marsh edge to the bay and recording the cover type present.

I used the neck-collar technique (Kluyver 1933) to obtain dietary samples from nestling Seaside Sparrows. This technique is more reliable than stomach analysis, which can be difficult and often misleading because soft-bodied foods digest more rapidly than harder, more sclerotized items. More importantly, the use of the neck-collar technique eliminates the need to sacrifice nestling birds, which is inherent in stomach analysis. Volumetric dietary data must be treated with caution however, for samples collected from nestlings after 1 hour may be biased in relation to (1) the mean volume of food delivered to each nestling per hour and (2) the size of individual food items (Johnson et al. 1980). Thus, these data are used as indices to compare the food habits of Seaside Sparrows in the two study areas, and are not meant as absolute numbers. The "ligature method" does not seem to appreciably affect diet composition (Johnson et al. 1980).

I found active nests by flushing an adult from the vicinity of the nest, or by observing an adult bird entering the vegetation with food for its young. I marked the location of each nest by inserting a *Phragmites* stem into the marsh substrate, 1 m E of the nest. When the nestlings in any nest were at least 3 days old, I began to

sample their diets. I fastened a ligature (pipe-cleaner) around the throat of each nestling to prevent the bird from swallowing. After a 1-hour sampling period, I returned to the nest and recovered the delivered food items trapped in the nestling's mouth cavity and esophagus. In addition, I examined the nest cup and the ground in the vicinity of the nest for any regurgitated food items. I recorded the following information: date, time, nest contents, number of nestlings collared, and the number of nestlings from which I recovered food. I inserted these data and the food items into a vial filled with 70% ethanol. Most of the dietary samples were collected during the midday hours (0900 to 1600).

Because nestling birds tend to leave the nest prematurely when disturbed (Woelfenden 1956), I placed wire, hardware-cloth corrals in the vegetation around each nest to contain the young. The corrals enabled me to obtain dietary samples from older young, and to collect a daily series of dietary samples from individual nests over a longer period of time than would otherwise have been possible. Post (1981) found that the frequency of nest visitation did not affect nest success.

I identified most food items to the family level (Orians and Horn 1969) with the aid of a binocular dissecting microscope and keys (Borror et al. 1976; Peterson 1948, 1951). Some of the more important dietary specimens were identified to the generic or specific level by taxonomists at the Insect Identification and Beneficial Insect Introduction Institute, U.S. Department of Agriculture, Beltsville, Maryland, and the Department of Entomology, North Carolina State University, Raleigh, North Carolina. I determined food volume by water displacement (Best 1974). I used Duncan's multiple range test (Barr et al. 1978) to compare the volumes of food delivered to nestling Seaside Sparrows of various ages in each salt marsh. I calculated the diversity of nestling diets according to Brillouin's (1956) formula:

$$H = (1/N) \left(\log_{10} N! - \sum_{i=1}^S \log_{10} N_i! \right),$$

where N is the total number of individuals, N_i is the number of individuals in the i^{th} species, and S is the number of species. I assigned the dietary specimens to a ground or vegetation category based on their occurrence in core samples of the marsh substrate or sweep samples of the vegetation, respectively (Merriam 1979). I used the Chi-square test (Snedecor and Cochran 1967) for statistical analysis of different vertical foraging patterns between Seaside Sparrows in the two salt marshes based on the predicted location of their selected foods.

RESULTS

The number and volume (cc) of invertebrates in food samples collected from nestling Seaside Sparrows at Oak Beach and West Gilgo, New York, are shown in Table 2. Nestling Seaside Sparrows in both marshes consumed a wide variety of invertebrates, but mainly insects. Although nestling Seaside Sparrows at Oak Beach ate more types (36) of invertebrates than did nestling Seaside Sparrows at West Gilgo (25), their indices

TABLE 1. Percent of cover for various patch types at Oak Beach (unaltered salt marsh) and at West Gilgo (ditched salt marsh), New York, in 1978.

Cover type	Unaltered salt marsh ¹	Ditched salt marsh ²
<i>Spartina alterniflora</i>	47.8	22.6
Salt-meadow grasses (<i>S. patens</i> , <i>Distichlis spicata</i>)	2.2	23.1
Mixed salt-meadow grasses and <i>S. alterniflora</i>	5.2	27.4
<i>Salicornia europaea</i> , mixed <i>S. europaea</i> /other grasses	16.6	5.2
<i>Phragmites communis</i> , <i>Iva frutescens</i> , or wrack	8.2	10.6
Mud pools	3.9	0.2
Deep pools and ditches	16.2	10.9

¹ Estimates of percent of cover are based on maps of 217 plots, each 25 m².

² Estimates of percent of cover are based on five transects, 250 m long.

TABLE 2. The number and volume (cc) of invertebrates in food samples collected from nestling Seaside Sparrows at Oak Beach (unaltered salt marsh) and at West Gilgo (ditched salt marsh), New York, during 1978.

Prey taxa	Life stage ¹	Oak Beach marsh		West Gilgo marsh		Prey taxa	Life stage ¹	Oak Beach marsh		West Gilgo marsh	
		No.	Vol.	No.	Vol.			No.	Vol.	No.	Vol.
COLLEMBOLA	A	1	Tr ²	-	-	<i>T. lineola</i> (Fabricius)	P	-	-	4	.380
ORTHOPTERA						<i>Chrysops atlanticus</i> (Pechuman)	A	1	.051	-	-
Tettigoniidae							L	1	.095	-	-
<i>Conocephalus</i> sp.	A/N	-	-	3	.081	Dolichopodidae	A	5	.025	-	-
HEMIPTERA							L	2	.012	-	-
Saldidae						Syrphidae	A	4	.508	-	-
<i>Pentacora sphacelata</i> (Uhler)	A/N	1	.004	3	.012		L	3	.330	-	-
Miridae						Otitidae	A	1	.010	-	-
<i>Trigonotylus tarsalis</i> (Reuter)	A/N	41	.127	6	.019	Ephydriidae	A	42	.420	-	-
Nabidae							L	4	.040	-	-
<i>Nabis</i> sp.	A/N	4	.040	-	-	HYMENOPTERA					
Pentatomidae						Chalcididae	A	3	.012	-	-
<i>Rhytidolomia saucia</i> (Say)	N	-	-	2	.040	Undetermined	A	2	.010	-	-
HOMOPTERA						ARANEIDA					
Cicadellidae	A/N	-	-	6	.142	Lycosidae	A	-	-	4	.092
Delphacidae	A/N	2	.001	2	.001		E	1	.028	3	.079
COLEOPTERA						Gnaphosidae	A	-	-	1	.010
Carabidae						Salticidae	A	-	-	1	.007
sp. of Pterostichini ?	L	1	.010	-	-	Dictynidae	A	2	.003	1	.002
Hydrophilidae						Undetermined	A	-	-	3	.019
<i>Enochrus</i> sp.	L	12	.048	2	.008	ACARI					
Melyridae						Undetermined	A	-	-	3	.004
<i>Collops</i> sp.	A	1	.013	-	-	AMPHIPODA					
Coccinellidae	L	1	.010	-	-	<i>Orchestia</i> sp.	A/J	3	.155	2	.020
Curculionidae	A	-	-	4	.020	ISOPODA					
LEPIDOPTERA						Undetermined	A	4	.016	-	-
Pylalidae	A	7	.210	1	.030	GASTROPODA					
Noctuidae						Undetermined	A/J	11	.010	3	.015
sp. of Herminiinae	L	13	.923	-	-	TOTAL		238	6.288	91	3.681
Undetermined	P	-	-	1	.081						
	L	2	.420	-	-	Number of nests sampled		238		91	
DIPTERA						Prey diversity					
Tipulidae	A	8	.070	-	-	$H = (1/N) (\log_{10} N! - \sum_{i=1}^S \log_{10} N_i!)$		1.15		1.12	
Ceratopogonidae	L	3	.009	-	-						
Chironomidae	A	1	.004								
Stratiomyidae											
<i>Odontomyia microstoma</i> (L.W.)	A	29	.957	6	.198						
	L/P	7	.433	2	.196						
Tabanidae											
<i>Tabanus nigrovittatus</i> (Macquart)	A	1	.068	13	.884						
	L	4	.264	2	.106						
	P	10	.950	13	1.235						

¹ Life stages are denoted by the letters: A (adult), E (egg case), J (juvenile), L (larvae), N (nymph), and P (pupae).

² Volumes of less than 0.001 cc are identified by the letters "Tr" (trace).

of prey diversity were similar (Oak Beach, $H = 1.15$; West Gilgo, $H = 1.12$).

The percent of composition by number of the major food items fed to nestling Seaside Sparrows in the two salt marshes during 1978 are shown in Figure 1. At Oak Beach, the most frequently taken orders were the Diptera (52.9%), mainly adult Ephydriidae and adults and larvae of the stratiomyid *Odontomyia microstoma*, and the Hemiptera (19.3%), mainly nymphs and adults of the mirid *Trigonotylus tarsalis*. At West Gilgo, the most frequently taken orders were the Diptera (44%), mainly immatures and adults of the tabanid *Tabanus nigrovittatus*, and the Araneida, mainly Lycosidae. The major quantitative differences between the diets of nestling Seaside Sparrows in the two salt marshes are: (1) nestling Seaside Sparrows at Oak Beach ate a wider variety of Diptera (nine families), Lepidoptera (mainly Noctuidae), and Hemiptera than did nestling Seaside Sparrows at West Gilgo, and (2) nestling Seaside Sparrows at West Gilgo ate a higher proportion of immature and adult Tabanidae, Arachnida, and Coleoptera than did nestling Seaside Sparrows at Oak Beach.

Frequently, the individual food items were altered by parent Seaside Sparrows prior to being fed to their nestlings. Hemiptera and adult Lepidoptera often lacked one or more legs. Lepidoptera and Diptera larvae were usually delivered intact, but parent birds apparently masticated large larvae to aid ingestion by the nestlings. Most adult Diptera and small Homoptera were delivered intact. Araneida often lacked a full complement of legs and sometimes only the abdomen was delivered to the nestlings.

Most of the food samples I collected from nestlings at both marshes contained more than one food item or type of items. These food samples were aggregates of individual food items that were held together by mucous in the nestling's mouth cavity. I was unable to determine if this food bolus formed within the mouth cavity of the nestlings because of their inability to swallow, or if the assemblage was made by parent birds as an efficient means of carrying and delivering many small prey items. The formation of a food bolus, however, increased the efficiency of the neck-collar technique, enabling me to collect small-sized food specimens that might have otherwise slipped past the point of constriction imposed by the neck-collar on each nestling.

The energetic importance of the food items fed to nestling Seaside Sparrows is better represented by volumetric than by numerical analysis. Figure 2 shows the percent of composition by volume for the major foods fed to nestling Seaside Sparrows at Oak Beach and West Gilgo during 1978. The importance of certain food items, as measured by their numerical occurrence, has been either amplified or diminished by the volumetric analysis. Although a large number of Hemiptera (Miridae) and Ephydriidae appear in the diet of nestling Seaside Sparrows at Oak Beach, the small volumes of these insects limit their energetic importance. Because of their relatively large volumes, the Lepidoptera (Noctuidae), Stratiomyidae, Tabanidae, and Syrphidae consumed by nestling Seaside Sparrows at Oak Beach, however, are more important in the diet of the nestlings than their numbers would seem to indicate. Volumetric analysis of the food items of nestling Seaside Sparrows

at West Gilgo also altered the importance of certain food items. Arachnida, Hemiptera, and Homoptera are diminished in importance, whereas Tabanidae (immature and adult) increased in importance as compared to their numerical occurrence.

Although the volumetric analysis altered the importance of certain food items in relation to the numerical data, most of the differences between the diets of nestling Seaside Sparrows at Oak Beach and at West Gilgo elucidated by numerical analysis persist. Diptera remain the most important food source for nestling Seaside Sparrows at both study areas. Adult and immature Tabanidae (70.8% of total volume) remain the most important food of nestling Seaside Sparrows at West Gilgo, but at Oak Beach nestling Seaside Sparrows rely most heavily on Stratiomyidae, Tabanidae, and Lepidoptera (22.1%, 22.7%, and 24.7% of total volume, respectively).

The size of foods given to nestling Seaside Sparrows of various ages at Oak Beach and West Gilgo ranged from less than 0.005 cc to 0.22 cc (Fig. 3 and 4). At Oak Beach, the frequency of food items smaller than 0.01 cc decreased in the diet of nestlings as they grew older (Fig. 3), although these food items (mainly Miridae) continued to be fed to older nestlings. Food items with volumes greater than 0.05 cc occurred more frequently in the diet as the nestlings grew older. At West Gilgo, the percentages of the food items of various volumes fluctuated among the age groups of nestlings (Fig. 4). The percentage of small-sized food items (less than 0.01 cc) in the diet increased from age groups 3-4 (days) to 5-6, decreased from age groups 5-6 to 7-8, and increased again from age groups 7-8 to 9-10. Thus, in contrast to the trends observed at Oak Beach, nestling Seaside Sparrows at West Gilgo showed no apparent age-related trends in the distribution of different-sized food items.

The mean (minimal) volumes of food (cc) delivered to nestling Seaside Sparrows of various ages at Oak Beach and West Gilgo are shown in Table 3. At Oak Beach, the volume of food delivered to nestling Seaside Sparrows appeared to increase with the increasing age of nestlings. Although the increase in the volume of food delivered to nestlings between age classes 3-4 and 5-6 was not significant ($p > .05$), the increase between age classes 5-6 and 7-8 was significant ($p < .05$). The volume of food delivered to nestlings 9 and 10 days old was not significantly different ($p > .05$) from the volumes of food delivered to nestlings of any of the other age classes. At West Gilgo, there was no significant difference ($p > .05$) between any of the age classes in respect to the mean volume of food delivered per class.

The differences between the diets of nestling Seaside Sparrows at Oak Beach and West Gilgo are indicative of the foraging patterns of parent birds. The number and percentage of prey items in the diets of nestling Seaside Sparrows normally found on the ground or on the vegetation at Oak Beach and West Gilgo are shown in Table 4. Parent Seaside Sparrows in the two salt marshes differ significantly ($p < .005$) in their vertical use of habitat for foraging. At Oak Beach nestling Seaside Sparrows consumed 23.3% more prey items from the vegetation column than did nestlings at West Gilgo. At West Gilgo, parents took almost equal amounts of prey

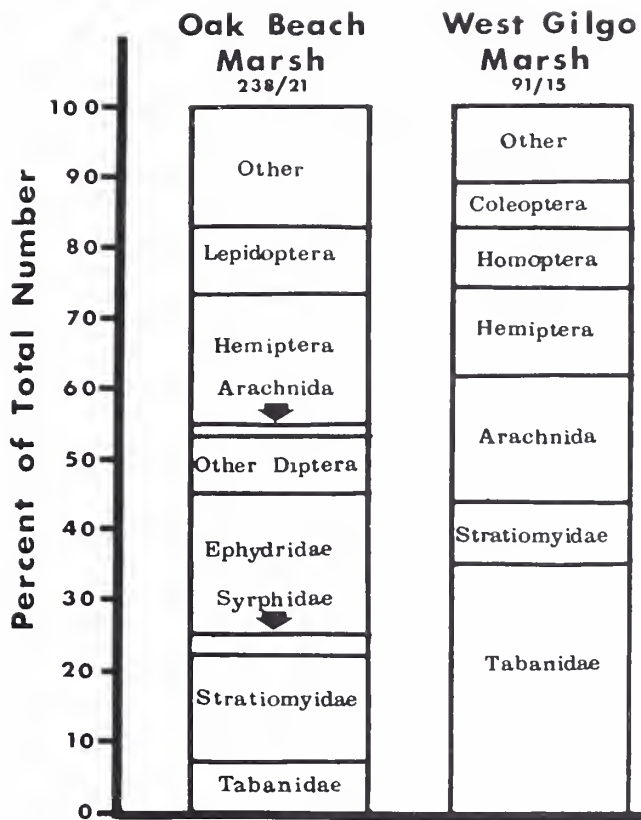


Fig. 1. The percent of composition by number of the major food items fed to nestling Seaside Sparrows at Oak Beach (unaltered salt marsh) and West Gilgo (ditched salt marsh), New York, during 1978. The numbers above the graph indicate the number of food items (numerator) and the number of nests sampled (denominator) included in the analysis.

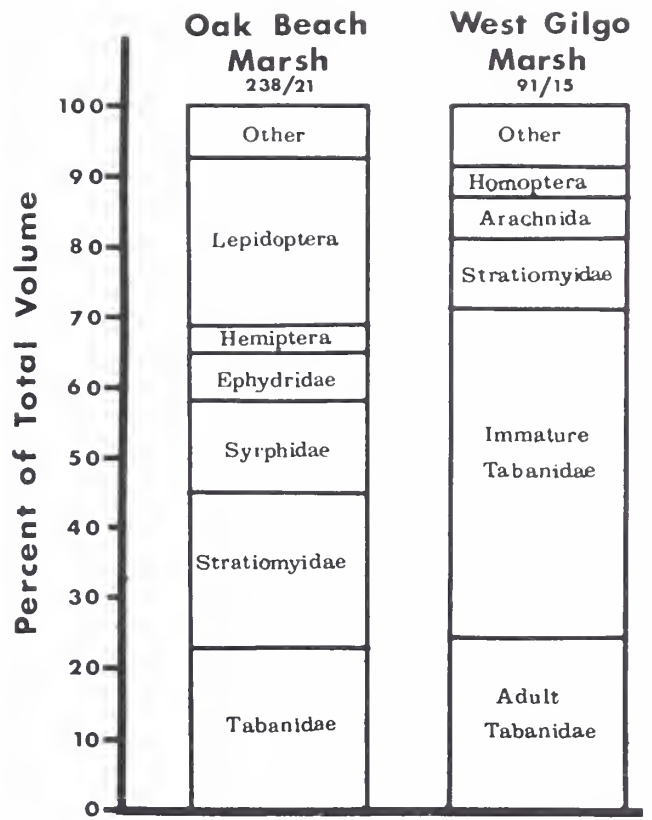


Fig. 2. The percent of composition by volume (cc) of the major food items fed to nestling Seaside Sparrows at Oak Beach (unaltered salt marsh) and West Gilgo (ditched salt marsh), New York, during 1978. The numbers above the graph indicate the number of food items (numerator) and the number of nests sampled (denominator) included in the analysis.

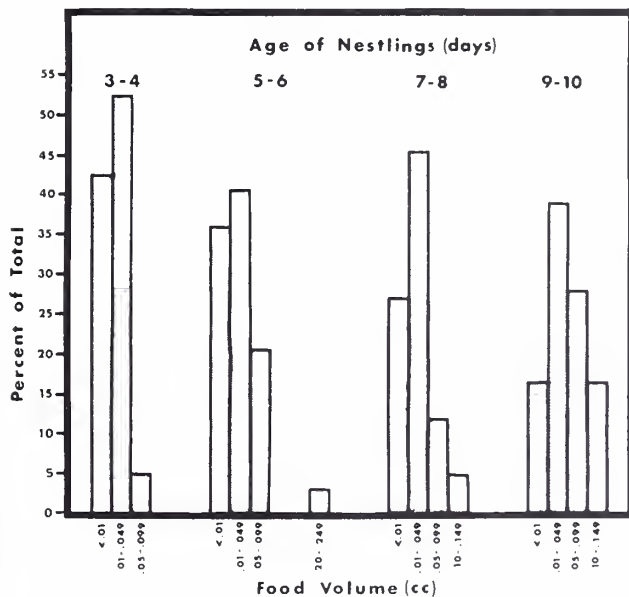


Fig. 3. Size distribution of individual food items collected from nestling Seaside Sparrows of various ages at Oak Beach (unaltered salt marsh), New York, during 1978.

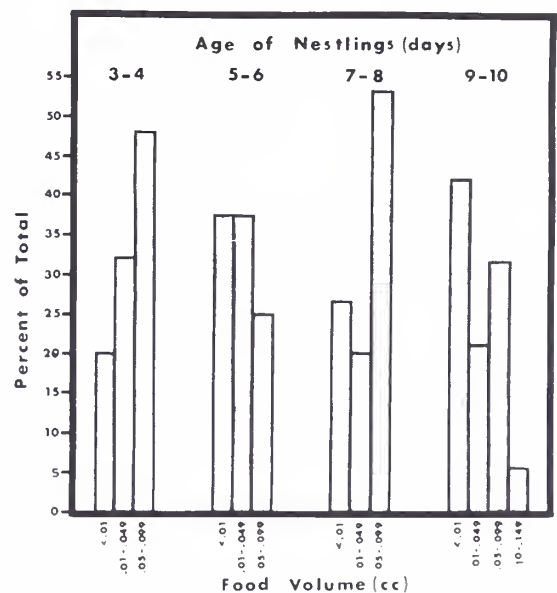


Fig. 4. Size distribution of individual food items collected from nestling Seaside Sparrows of various ages at West Gilgo (ditched salt marsh), New York, during 1978.

TABLE 3. Volume of food (cc) delivered per hour to nestling Seaside Sparrows of various ages at Oak Beach (unaltered salt marsh) and at West Gilgo (ditched salt marsh), New York, in 1978.

Nestling age (days)	Mean volume of food (cc)/hour per nest ¹	
	Unaltered salt marsh	Ditched salt marsh
3 - 4	.0370a	.0874a
5 - 6	.0910a	.0553a
7 - 8	.2526b	.0924a
9 - 10	.1000ab	.0783a

¹ Within each type of salt marsh, means with a common letter are not significantly different at the 0.05 level (Duncan's multiple range test).

from the ground and the vegetation, but at Oak Beach most of the food delivered to nestlings (70.6%) was taken from the vegetation column.

It is important to note that the prey species assigned to the ground location (Diptera larvae, Coleoptera larvae, and Amphipoda) are behaviorally restricted to this type of habitat, whereas the majority of the prey items assigned to the vegetation column location are active organisms (adult Diptera, Hemiptera, Homoptera, and Arachnida) and may have been captured on the surface of the marsh soil. Therefore, the percent values given in Table 4 represent the maximal difference in the amount of vertical habitat use within each study area.

DISCUSSION

The diets of nestling Seaside Sparrows in salt marshes at Oak Beach and West Gilgo, N.Y., are similar in nature to the diets of nestlings of other species of emberizine sparrows. Evans (1964) found that nestling Vesper Sparrows (*Poocetes gramineus*), Field Sparrows (*Spizella pusilla*), and Chipping Sparrows (*S. passerina*) in southeastern Michigan ate insectivorous diets. Best (1974) confirmed Evans's (1964) findings in regard to the diet of nestling Field Sparrows. Robins (1971) reported that 97% of the diet of nestling Henslow's Sparrows (*Ammodramus henslowii*) consisted of insects. In addition, nestling Song Sparrows (*Melospiza melodia*) rely heavily on insects as food (Tompkins 1962).

The proportions of the major taxa in the diet of nestling Seaside Sparrows reported in this study are similar to those reported by Post (1974) for nestling Seaside Sparrows in the unaltered salt marsh at Oak Beach during 1970 and 1971. In both studies, Hemiptera and Diptera were the most frequent foods in the nestlings' diet. During this study, however, nestling Seaside Sparrows consumed a lower proportion of Lepidoptera and Trichoptera than reported by Post (1974).

In the altered salt marsh at West Gilgo, the proportions of the major taxa in the diet of nestling Seaside Sparrows reported in this study were very different from those reported by Post (1974). Post reported that 75.2% of the diet of nestling Seaside Sparrows was composed of Lepidoptera and Trichoptera, and 17.5% Diptera. In this study, the diet of nestling Seaside Sparrows at West Gilgo consisted of 44% Diptera and only about 2% Lepidoptera. These different findings for

TABLE 4. Number and percentage of food items of nestling Seaside Sparrows normally found on the ground or on the vegetation at Oak Beach (unaltered salt marsh) and at West Gilgo (ditched salt marsh), New York, during 1978.

Vertical location of food resource ¹	Unaltered salt marsh		Ditched salt marsh	
	Number	Percent	Number	Percent
Ground	70	29.4	48	52.7
Vegetation	168	70.6	43	47.3

$X^2 = 11.22$ ($p < .005$)

¹ Food items were grouped in *Ground* location if found in core samples of marsh substrate, or in *Vegetation* location if found in sweep samples (see Merriam 1979).

the major taxa brought to nestling Seaside Sparrows in altered salt marshes may be due to Post's having studied their diets in two ditched salt marshes (West Gilgo and Tobay). In addition, these inconsistent data may be related to different sample sizes, or changes in the availability or use of food resources.

Johnson et al. (1980) reported that the neck-ligature technique is biased in favor of smaller food items in the case of older nestlings, because older nestlings tend to disgorge larger-sized foods, which are either eaten by parent birds or removed from the nest. I observed nests containing ligatured young and found no evidence that parent Seaside Sparrows were taking food items away from their nests. In addition, I recovered disgorged food items from Seaside nests on many occasions. Nonetheless, parent Seaside Sparrows may have eaten some disgorged food items. If one assumes that the biases associated with the "ligature method" reported by Johnson et al. (1980) were operating during this study, the distribution of food items of various sizes and the total volume of food delivered among the various age classes of nestling Seaside Sparrows at Oak Beach and West Gilgo are minimal, and thus dietary differences among nestling age classes may be greater than those reported (Fig. 3 and 4, Table 3).

The fragmentation and partial mastication of food items by adult Seaside Sparrows is not unique. This type of behavior has been observed in other bird species (Stewart 1953, Tinbergen 1960, Best 1974). Some of the food items delivered to nestling Seaside Sparrows at both study areas probably lost their wings, legs, or other body parts during capture. Adult sparrows may have chewed and beaten large prey in order to kill them, though some were probably altered to facilitate ingestion by the nestlings. Woolfenden (1956) observed adult Seaside Sparrows clipping the wings from adult Lepidoptera.

The composition of the diets and the contrasting vertical foraging patterns of Seaside Sparrows in unaltered and ditched salt marshes is probably related to the habitats in which parent birds forage and to the types and numbers of invertebrates available in these habitats. Merriam (1979) reported that at Oak Beach, Seaside Sparrows foraged throughout the marsh, especially in areas of *S. alterniflora* (48% of the total vegetation cover). Adult Seaside Sparrows spent 30% of their

time (assumed foraging) in mud pool/*S. alterniflora* sites and 38% in mucky areas of the marsh where *S. europeae* and *S. alterniflora* grow. Adult and larval Stratiomyidae, Ephydriidae, and Miridae were numerous in these areas (Merriam 1979). In ditched salt marshes, Post (1974) found that Seaside Sparrows had restricted feeding areas, in that male Seaside Sparrows spent 39% of their time foraging in *Iva* or wrack (only 8.2% of the total vegetation cover), and 27% along ditches (7.8% of the total vegetation cover). While *S. alterniflora* marshes are the major source of tabanids (Axtell 1976), salt marshes that are ditched for mosquito control can have greater expanses of suitable habitat for tabanid larvae (areas subject to alternate drying and flooding) (Bailey 1948). Because tabanids are abundant along drainage ditches in altered marshes (Rockel and Hansens 1970), it is not surprising that tabanids constitute a major portion of the diet of nestling Seaside Sparrows at West Gilgo. In addition, spiders (mainly Lycosidae) are very common in salt-meadow grasses (Barnes 1953), and thus constitute a major portion of the diet of nestling Seaside Sparrows at West Gilgo.

Compared to parent Seaside Sparrows in the ditched salt marsh, those in the unaltered salt marsh are capable of delivering larger-sized foods and a larger total volume of food to older nestlings. This may indicate that food resources in the unaltered salt marsh are abundant and diverse enough to allow parent Seaside Sparrows to encounter and capture prey of different sizes, thus giving them the opportunity to be more discriminating in their selection of food items than Seaside Sparrows at West Gilgo. Davis and Gray (1966) reported that insect productivity may be correlated with the amount of *S. alterniflora* in a given area. The Oak Beach study area had 25.2% more *S. alterniflora* than did the West Gilgo study area (Table 1). In addition, the unaltered salt marsh at Oak Beach had extensive areas of *S. europeae* and *S. alterniflora*, which support large invertebrate populations (Merriam, unpubl. data).

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Comparative Ecology of Northern and Southern Populations of the Seaside Sparrow

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Abstract. We compare the ecology during the breeding season of Seaside Sparrows (*Ammospiza maritima*) in New York and Florida. The foraging behavior and diet specialization of both groups were similar. Birds in Florida took food almost entirely from vegetation. New York birds gleaned and probed mud frequently. The difference in foraging behavior between regions were based on prey availability. The diversity of food brought to nests in Florida was higher than in New York, a difference related to higher arthropod diversity in the southern marsh. New York nest sites had the same characteristics as randomly chosen points. Florida birds used vegetation less tall and dense than in the whole marsh, a difference resulting in part from competition with Rice Rats (*Oryzomys palustris*). In Florida 3% of eggs produced fledglings, compared to 35% in New York, a difference related to greater predation by rodents in Florida. Most nest destruction in New York came from flooding. Over the 2-year period females in New York produced seven times as many young per year as did Florida females. Low reproductive success in Florida was balanced by high (86%) annual survival of adults. Minimum adult survival in New York was 58%. Replacement rates indicate that during the period of the study the Florida population was stable, while the New York population was increasing. In both regions all pairs that we studied were monogamous, and sexes defended nest-centered territories. Both sexes foraged in their defended area as well as on communal feeding grounds. In both areas males delivered food to nestlings at the same rate as did females. Females were able to compensate for lack of male aid. Monogamy is probably maintained because of its association with territorial behavior, which leads to reduced nest density and thus predation. We conclude that the Seaside Sparrow is opportunistic throughout its range, but that its behavior is constrained by a temporally heterogeneous environment.

Seaside Sparrows (*Ammospiza maritima*) are residents in coastal salt marshes from Massachusetts to Texas. Although widespread, their specialized habitat requirements restrict them to narrow coastal zones. Most populations do not nest more than a few kilometers from the sea. The distribution of the species is interrupted at frequent intervals by large bays and inlets as well as by disturbances from human activities.

Various populations of the Seaside Sparrow have become extinct or rare because of habitat alterations associated with the activities of humans (Sharp 1970, Baker 1973, Werner 1975, Sykes 1980). All of the survival problems confronting the narrowly distributed Atlantic Coast groups of the Seaside Sparrow are accentuated in Florida, because of the Florida population's location at an extremity of the species' range, its greater isolation, and its smaller size. The situation is exemplified by the status of *A. m. nigrescens* and *A. m. mirabilis*.

Such isolated groups are prone to stochastic extinction by agencies such as hurricanes or fires.

Because Seaside Sparrows live in relatively inaccessible habitats, they have not been regularly studied over most of their range. Other than studies in the Northeast, in New Jersey (Woolfenden 1956) and New York (Post 1974, Post and Greenlaw 1975), little is known of the breeding biology of the species.

The Seaside Sparrow is a good subject for studies of geographic variation in life-history features. The species occupies a structurally simple habitat, and the vegetation of this habitat converges in form over a wide geographic range. Only several other Passeriformes have colonized salt marshes, and the Seaside Sparrow has few avian competitors. These simplifying elements may allow more meaningful comparisons between populations regarding the effects of variables such as food supply, predation, and latitude. We concentrate on the

following questions:

- (1) How does feeding behavior vary between regions, and how is it related to food supply?
- (2) How do Seaside Sparrows in the different regions use the habitat for nesting?
- (3) How does nesting success vary regionally, and if there is significant variation, what are its causes?
- (4) What are the demographic characteristics of each population?

STUDY SITES

New York: A northern population was studied at Oak Beach (40°38'N) in a salt marsh bordering the southern shore of Great South Bay. The shoreline is gradual, and tides on the bay average about 0.6 m. In the central section of the marsh, water levels usually vary no more than 30 mm, and are influenced more by winds than by tides. During rainless periods the salinity of the central marsh is 26 to 30 parts per thousand.

Vegetation covers 80% of the site, while the rest is covered by bay inlets and pools. Smooth Cordgrass (*Spartina alterniflora*) accounts for 60% of the vegetative cover, the remainder being Glasswort (*Salicornia europea*), 21%; salt meadow grasses (*Spartina patens* and *Distichlis spicata*), 9%; Reed (*Phragmites australis*), 9%; and wrack, 2%. The study area extends landward from the bay for 250 to 400 m, meeting a 10- to 30-m corridor of salt meadow grasses, which abruptly joins a stand of *Phragmites*, 30 to 50 m wide. Although no tidal creeks intersect the marsh, it is dotted with shallow pools and mud flats. More detailed descriptions are available (Post 1970a).

Florida: A population near the southern end of the species' range was studied in Gulf Hammock (29°11'N) on Waccasassa Bay, an extension of the Gulf of Mexico. The shoreline of this salt marsh is gradual, but dotted with oyster bars and small islands, and cut by creeks. The study site is flat, except for creeks up to 2 m deep. Tides average 0.8 m. The average salinity is $19.03 \pm$ (SE) 1.09 ‰ (32 stations on 24 April). Low tide exposes extensive mud banks, riddled with burrows of crabs (*Uca* and *Sesarma*). Vegetation covers 94% of the study area, and tidal creeks cover 6%. Vascular plants, in order of importance (percent of relative cover) were *S. alterniflora*, 38%; Black Needlerush (*Juncus roemerianus*), 26%; Seashore Saltgrass (*Distichlis spicata*), 23%; Glasswort (*Salicornia virginica*), 8%; Saltwort (*Batis maritima*), 3%; Sea Oxeye (*Borrchia frutescens*), <1%; Virginia Dropseed (*Sporobolus virginicus*), <1%; Sea Lavender (*Limonium carolinianum*), <1%; Christmas Berry (*Lycium carolinianum*), <1%; Key Grass (*Monanthochloe littoralis*), <1%; Salt-marsh Aster (*Aster tenuifolius*), <1%; and wrack deposits, <1%. The relative elevation of the major plant communities is indicated by water depth (cm) during spring flood tide, where greater water depths signify lower elevations: *S. alterniflora* ($N = 11$), 25.6 ± 7.2 ; *J. roemerianus* (11), 20.9 ± 5.3 ; *B. maritima* (3), 16.5 ; *D. spicata* (31), 15.3 ± 3.3 ; *S. virginica* (6), 13.8 ± 1.2 .

METHODS

We conducted detailed work in New York during 1977 and 1978, and in Florida during 1979 and 1980. We continued banding and census work in New York

through 1980, in an effort to determine the survival of cohorts banded from 1967 through 1972.

At each site we established a 30-ha study area gridded with wooden stakes placed at 25-m intervals. We attached wire prongs to the tops of stakes to discourage their use by predatory birds.

We captured birds throughout the year, giving individuals unique combinations of colored bands. During the breeding period we sexed birds by presence of a cloacal protuberance (males) or brood patch (females). We mapped the home ranges of marked birds by recording their position in relation to the grid. We determined the sizes of activity spaces by plotting positions on maps and connecting the outer points to form the largest possible polygon. To determine survival, we searched for marked individuals, and also employed mist nets. Disappearance from the censuses is equated with death (Haartman 1971).

We found most nests in both areas, marking them with reed stems placed low in the grass, 1 to 2 m from the nest. Based on the Florida data, frequency of nest visitation did not affect nest success (Post 1981). We correct our estimates of nest survival by considering the period that they were exposed to risk (Mayfield 1975, Johnson 1979). We randomly chose some nests for studies of nestling foods and growth rates. In New York, when the young were about 7 days old, we put hardware-cloth cylinders around their nests. As the young fledged on about the eighth day (time of hatching = day 0), these retaining corrals enabled us to collect information through 10 days of age. In Florida, predation by Rice Rats (*Oryzomys palustris*) required us to use galvanized metal cylinders to protect nests containing the young used for sampling food. The periods that nests were encircled with cylinders were excluded from our calculations of nesting success.

We collected food samples from nestlings older than 3 days by placing a pipe-cleaner ligature around their throats (Orians and Horn 1969). After an hour we retrieved the food from the young, or from the nest cup. We calculated diversity of nestling diets by Brillouin's formula (Hurtubia 1973):

$$H = \frac{1}{N} (\log_{10} N! - \sum_{i=1}^S \log_{10} N_i!),$$

where N is the total number of prey individuals, N_i is the number of individuals in the i th species, and S is the number of species. As the contents of separate food samples are successively pooled, the accumulated trophic diversity (H_k) approaches stability at some point (t) for the predator population (Hurtubia 1973). We calculated the average trophic diversity (H_{pop}) of the population with its variance and standard error using values of H_k for $K > t$.

We determined food availability by: (1) sweeping the vegetation with 38-cm-diameter insect nets; (2) sampling organisms inhabiting the mud with metal cylinders (35 cm² in New York; 200 cm² in Florida). The resulting mud cores we then extracted in a Tullgren funnel (Macfayden 1953), or washed through fine screen, to retrieve invertebrates.

We sampled vegetation during the period when most pairs were carrying out their first nesting attempts



Fig. 1a.



Fig. 1b.



Fig. 1c.

Fig. 1. (a-c): Study site at Gulf Hammock, Florida. (a) Tidal creek bordered by *Spartina alterniflora* (background) and a mixture of *S. alterniflora*, *Distichlis spicata*, and *Batis maritima* (foreground), preferred foraging sites of Seaside Sparrows; (b) edge between *S. alterniflora* - *B. maritima* - *Salicornia virginica* (foreground) and *Juncus roemerianus* (taller vegetation in background); (c) ecotone between *D. spicata* (right) and *J. roemerianus* (left), a preferred nesting area of Seaside Sparrows at the Florida site.



Fig. 1d.



Fig. 1e.



Fig. 1f.

(d-f): Study site at Oak Beach, New York. (d) Medium-height *S. alterniflora* interspersed with small mud pools, microhabitats used most often by feeding Seaside Sparrows; (e) medium-height *S. alterniflora* used as nesting area by Seaside Sparrows (foreground). *Phragmites* and scrub (background) border the edge of the marsh; (f) nesting area bordering Great South Bay (background).

(April in Florida, June in New York). Across randomly chosen grid blocks we established diagonal transects, along which we randomly placed m^2 quadrats. The corners of the quadrats served as subpoints, at each of which we vertically positioned a thin metal rod divided into dm intervals. We then tallied the number of contacts that vegetation made with each dm. The plant species and its growth form (green or residual) were recorded for each contact with the rod. These methods follow those of Wiens (1969). In addition to the above measures, we classified each subpoint according to the numerically dominant plant species and its growth form.

We used the same procedure to sample the vegetation around nests, which served as the centers of the quadrats. The same data enumerated above were collected for the four points. In addition, we measured the height of nest contents above the substrate, and estimated the percentage that the top of the nest was hidden when viewed from above.

The degree of correspondence between the vegetation around nests and in the habitat as a whole (random points) was measured by discriminant function analysis (James 1971, Klecka 1975, Lachenbruch and Goldstein 1979). The objective of discriminant analysis is to weight and linearly combine the variables so that the groups are forced to be as statistically divergent as possible. The weighting coefficients serve to identify those variables that are most important in differentiating the functions. For each study site we derived one discriminant function, as two groups (nest-centered quadrats and randomly chosen quadrats) were being compared. Once a discriminant function was derived, as a check for the adequacy of the discriminating variables, each case was identified for likely group membership, using only the case's values on the discriminating variables. In addition to discriminant function analysis, which considers all variables simultaneously, we subjected each variable to a univariate test for intergroup difference (one-way analysis of variance).

The variables we used in these analyses were based on the average of each of the four subpoints in the quadrats. The variables used were: (1) maximum height of vegetation in the quadrat; (2) height (dm) at which the maximum number of contacts occurred, as determined by averaging contacts at all four subpoints; (3) average ratio of residual to green vegetation; (4) average number of contacts by residual vegetation; (5) average total number of contacts; (6) average number of contacts occurring in the dm with largest number of contacts; and (7) heterogeneity, defined for each quadrat as (maximum number of contacts at any point — minimum number of contacts at any point)/average number of contacts at all four points (Wiens 1974). We believe that these variables are appropriate to a grassland bird choosing a nest site. As in each year of the study we located at least 90% of the nests in both sites and as our sample sizes were large, we do not foresee any bias in our selection of nest quadrats for analysis. For randomly chosen quadrats, we did not sample vegetation types that were not used for nesting (e.g. *Phragmites* in New York, scrub edge in Florida).

To map activity spaces of birds, we used two procedures. (1) In New York we watched birds from elevated blinds, so that the observer's eyes were about 4 m above

ground. In this way, we could see 8 to 12 pairs from one position. (2) In Florida and New York we systematically crossed the grid, mapping the positions of singing or displaying males. In Florida, because of the larger territory sizes of the sparrows and the difficulty we had in crossing inlets, we divided the study site into an eastern and western section, and covered each section alternately.

RESULTS

Annual Cycle

The New York population was migratory, and by 1 November most individuals had left the marsh. Resident males returned in the last week of April, and females about a week later. The average date of initiation of first clutches was 19 May, whereas the average date of the last-clutch initiation was 20 July. The average median-clutch initiation date was 14 June. The average length of the breeding period, computed by the method of Ricklefs and Bloom (1977) was 75 days.

The Florida population was nonmigratory. In Florida the average date of the first egg was 23 March. The median date of clutch initiation in 1979 was 29 April. The corresponding figure in 1980 was 1 May. The last clutches were started on 15 June 1979 and 23 June 1980. The length of the breeding season (2-year average) was 96 days.

Foraging and Food

The most common method used by foraging birds was walking on the ground, gleaning insects from surrounding vegetation, usually by attacking prey that could be reached by extending the neck or by lunging short distances. Birds rarely hovered or flycatched. Individuals walking on the ground also probed and pecked the mud or whatever surface they were walking on. Birds chased elusive items. Less frequently used foraging positions were located above ground, where birds slowly walked or climbed through the grass, gleaning as they moved. Birds perched in vegetation also gleaned surrounding vegetation, or snapped the air. In New York, gleaning vegetation accounted for 35% of 282 foraging maneuvers, whereas gleaning or probing mud was used 38% of the time, gleaning wrack 11%, gleaning or probing water 10%, hovering or flycatching 4%, and chasing or lunging 2%.

In Florida, Seaside Sparrows foraged most frequently in *Spartina alterniflora* (Fig. 1), the vegetation that harbored most insects (Table 1). *Spartina* was used as a foraging site out of proportion to its representation on the marsh (Fig. 2). In contrast, *Juncus*, the most common cover type, was used less than expected. *Distichlis* was used infrequently for foraging, probably because of the difficulty that a ground-foraging bird would have in traversing the dense matrix of stems. In contrast, *Salicornia*, which was as attractive as *Distichlis* in terms of food abundance (Table 1), was used more often as a foraging site. *Salicornia* stands are open near the ground, and easily negotiated by ground-foraging sparrows. Other than its network of creeks, the Florida site had few open mud areas, such as were abundant in New York. However, in Florida many individuals foraged near creeks, either on their edges or in the bordering *S. alterniflora*. The average distance from water of

TABLE 1. The 10 most important invertebrate groups fed to nestling Seaside Sparrows, compared to their occurrence in the study area in Florida. These groups composed 85% by volume of the nestling diet.

Group	Nestling diet	Vegetation	% of group that was sweep-netted in:			
			Juncus	Spartina	Distichlis	Salicornia
Tettigoniidae	43.8 ¹	54.3 ²	12.5 ³	42.9	21.9	22.8
Lycosidae	22.9	18.8	11.9	55.1	13.3	19.9
Lepidoptera (Noctuidae and Pyralidae)	12.5	3.0	0	22.0	11.0	66.5
Other spiders	8.8	7.8	10.6	63.9	16.1	9.4
Delphacidae	3.9	3.6	11.9	58.9	21.5	7.8
Salticidae	3.1	4.9	4.9	64.8	14.6	16.0
Linyphiidae and Dictynidae	2.3	2.5	4.3	40.5	32.4	23.2
Amphipoda	1.5	0.2	0	23.1	0	76.9
Cicadellidae	0.6	3.6	2.6	12.1	57.7	27.5
Flattidae	0.6	1.2	2.3	18.2	4.5	75.0

¹ Percentage of total volume recovered from nestlings.

² Percentage of total volume obtained by sweep-netting.

³ Percent composition of total sweep-net sample, by vegetation type.

107 feeding birds was 4.9 m. In contrast, the average distance from *Juncus*, the cover where birds usually took refuge, was 27.7 m.

In New York, Seaside Sparrows foraged in *S. alterniflora* in proportion to its coverage of the area (Fig. 2). Except for the wrack, all other cover types were used less than would be expected if random choice alone was involved. In contrast, the sparrows used shallow pools or pool edges out of proportion to their availability (Fig. 2). This preference is a reflection of their main foraging method in New York: walking on the edge of open areas to glean from grass or from the substrate. Their use of this foraging method accounts for their avoidance of densely vegetated patches, such as *S. patens*.

In contrast to the possible range of food items that could be taken, Seaside Sparrows in Florida specialized on relatively few groups. The 10 most important groups (family or higher taxa) used for nestling food composed 85% of 552 items recovered. The remaining 15% were distributed among 47 groups. By volume, the most important invertebrate groups were long-horned grasshoppers (*Conocephalus* and *Orchelimum*), spiders (mainly Lycosidae), and moths (Noctuidae and Pyralidae).

In New York, Seaside Sparrows also used relatively few arthropod groups. The 10 most important groups fed to nestlings composed 94% of the volume. As measured by volume of food delivered to nests, flies (Stratiomyidae and Tabanidae) were most important, followed by moths (Noctuidae and Pyralidae) and then long-horned grasshoppers (Table 2). The birds in New York took large numbers of hemipterans, mainly Miridae (*Trigonotylus tarsalis*). Miridae were not common in Florida, but among smaller insects, many homopterans, mainly Delphacidae, were taken.

Other than several individual fiddler crabs (*Uca*), Seaside Sparrows in Florida took few mud-inhabiting invertebrates. In New York, birds obtained much of their food from mud: 14% of 1,203 nestling food items could be classified as strictly mud-inhabiting organisms,

TABLE 2. The 10 most common invertebrate groups fed to nestlings compared to their occurrence in the study area in New York. The groups composed 94% (by volume) of the diet.

Group	Nestling diet		Random samples	
	Vegetation ¹	Mud	Vegetation	Mud
Stratiomyidae	28.1 ²	62.4	3.6	51.5
Tabanidae	6.8	14.4	4.7	14.3
Noctuidae	24.8	—	5.6	1.5
Tettigoniidae	10.1	—	24.0	0
Amphipoda	—	23.2	0	29.7
Pyralidae	7.9	—	2.2	1.5
Libellulidae	6.6	—	1.0	0
Miridae	5.3	—	39.7	0.3
Araneida	5.2	—	15.2	1.3
Syrphidae	5.1	—	3.8	0

¹ Each invertebrate group was classified by substrate; e.g., immature flies were mud-inhabiting.

² Percentage of total volume.

such as immature flies. In contrast to the Florida marsh, flies were common in New York, and this was reflected in the Seaside Sparrow diet there. The bulk of the food brought to Seaside Sparrow nests in New York was composed of adult and immature flies of the families Stratiomyidae and Tabanidae. The stratiomyid *Odonotomyia microstomata* made up 33% of the volume of the food recovered from nestlings in New York, while the tabanids *Tabanus nigrovittatus* and *Chrysops* sp. accounted for 16% of the bulk. The production of Stratiomyidae in Florida salt marshes is probably low because their larvae are mud-inhabiting detritus-feeders, and in southern marshes litter and detritus are reduced rapidly by microorganisms (Cameron 1972). In addition, mud-inhabiting immature flies could be eaten by crustaceans at the Florida site. Cores taken from the mud in Florida throughout the summer of 1979 produced polychaetes and fiddler crabs, but few insects.

TABLE 3. Nest-site characteristics of Seaside Sparrows in New York and Florida, compared to random samples. Each sample represents a quadrat (4 sub-points).

	NEW YORK			FLORIDA		
	Nest (\bar{x} +SE) (N=94)	F (1,268)	Random (\bar{x} +SE) (N=176)	Nest (\bar{x} +SE) (N=47)	F (1,244)	Random (\bar{x} +SE) (N=199)
Maximum height of vegetation (dm)	5.44±0.13	1.85	5.22±0.11	7.19±0.21	5.25*	8.01±0.14
Heterogeneity	1.02±0.06	1.28	1.11±0.05	0.94±0.06	1.88	0.81±0.03
Density of Vegetation	7.62±0.31	1.03	6.20±0.30	9.42±0.43	0.79	10.46±0.21
Ratio of residual to green vegetation	1.57±0.23	0.84	1.96±0.28	1.62±0.23	2.88	1.93±0.07
Density of residual vegetation	3.71±0.24	0.58	3.48±0.21	5.56±0.32	6.90 **	6.53±0.16
No. of contacts in dm with most contacts	2.65±0.10	0.21	2.37±0.13	2.67±0.12	4.62 *	2.59±0.06
Dm with most contacts	1.98±0.12	0.01	2.69±0.14	2.83±0.21	5.56 *	3.58±0.16
Height (cm)	14.2±0.6	—	—	27.7±1.20	—	—
Percent nest covered from above	85.6±2.3	—	—	74.3±3.27	—	—
DFA parameters						
Eigenvalue		0.0511			0.1449	
Canonical correlation		0.2205			0.3557	
Chi-square statistics		13.2			32.5	
Significance (DF=7)		> 0.05			< 0.001	

* $P < .05$

** $P < .01$

The bulk of the food delivered to nests in Florida was composed of spiders and long-horned grasshoppers. Many spiders in Florida overwintered as adults, and Seaside Sparrows took a larger proportion of them early in the season. Grasshoppers were relatively uncommon early in the season, and their importance in the diet increased as the season progressed (Fig. 3). This same seasonal increase in the importance of Orthoptera was seen in New York. Probably at the time most young were becoming independent in both areas, grasshoppers made up the bulk of their food.

The degree of diet specialization in northern and southern Seaside Sparrow populations was close. For both groups the accumulated trophic diversity leveled off between 5 and 15 samples (Fig. 4). In New York H_{pop} was 1.08 ± 0.03 ; the corresponding value in Florida was 1.14 ± 0.03 (Fig. 4). The diversity of nestling diets was significantly higher in Florida than New York, and this was probably a reflection of the larger number of potential prey species in the southern marsh. Within an area, values of H can best be understood by comparison with values for other members of the community (Hurtubia 1973). As no other passerines occupied the Florida marsh during the summer, we have no other estimates of feeding-niche breadth there. Sharp-tailed Sparrows (*Ammodramus caudacuta*) nested in the New York marsh, and their degree of diet specialization was the same ($H_{pop} = 1.18 \pm 0.10$; $N = 26$) as our estimate for Seaside Sparrows in New York (Post and Greenlaw 1982). In addition, overlap in the diets of the two species was high (Post and Greenlaw 1982). The similarity in the two sparrows' diets indicates that food is not limited in the northern marsh.

Use of Nesting Habitat

Species occupying tidal marshes have limited vertical space in which they can place their nests. Spring tides occurring twice a month determine the lower point of successful nest placement. The upper point is determined by availability of stable vegetation for nest attachment and by the amount of cover above the nest. In the New York marsh appropriate nesting sites often were limited because of the destruction of *S. alterniflora* by winter storms (Post 1974). Birds returning in late April often were confronted with denuded territories. Also, Long-billed Marsh Wrens (*Cistothorus palustris*), Sharp-tailed Sparrows, and Red-winged Blackbirds (*Agelaius phoeniceus*) used similar sites. In Florida, marsh vegetation was relatively stable throughout the year, but Seaside Sparrows still faced the problem of limited vertical sites. Although no other avian species competed for nest sites in the southern marsh, Seaside Sparrow habitat choice was determined in part by interactions with Rice Rats (see below).

For each study area we compared the structure of vegetation surrounding Seaside Sparrow nests with that of vegetation at randomly chosen points (Table 3). For the New York site, none of the variables, considered singly (ANOVA) or jointly (DFA), enabled us to differentiate Seaside Sparrow nest sites from randomly chosen positions. In Florida we were able to separate nest quadrats from random quadrats using both techniques: analyzed singly, four of seven of the variables were different for the two groups. Considering all seven variables simultaneously, Florida Seaside Sparrow nest sites were significantly different from the overall habitat, as indicated by eigenvalue, canonical correlation,

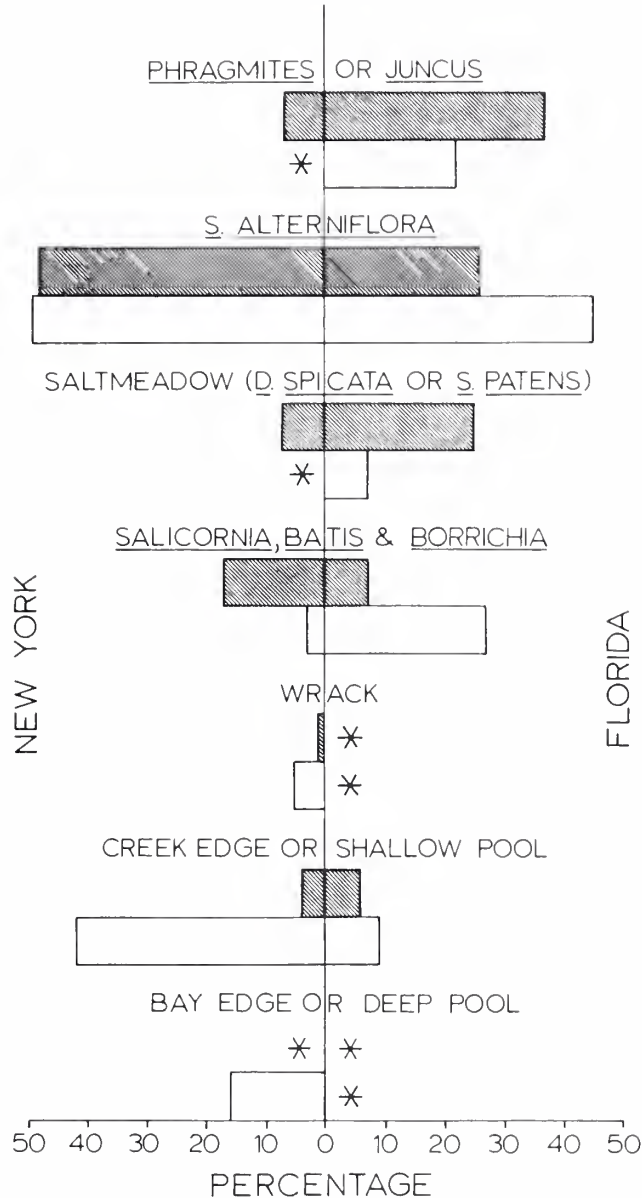


Fig. 2. Use of microhabitats for foraging by Seaside Sparrows in New York and Florida. Shaded bar = % of area available to foraging birds (sample size: N.Y., 217 cover plots, each 625 m²; Fla., 759 randomly placed points). Open bar = percentage of total observations that birds were recorded foraging in each microhabitat (sample size: N.Y., 424 observations; Fla., 267 observations). Asterisks in place of open bars indicate that microhabitats were used less than 1% of time. Asterisks in place of shaded bars indicate that microhabitats composed less than 1% of available area.

Fig. 4. Plots of accumulated trophic diversity (H_k) versus total food samples from counts of individual nests (K) for nestlings in New York (1977) and Florida (1979). Accumulated trophic diversities of each population are calculated for values of H_k for $K \geq t$ (arrows). In New York $H_{pop} = 1.08 \pm 0.03$; in Florida $H_{pop} = 1.14 \pm 0.03$.

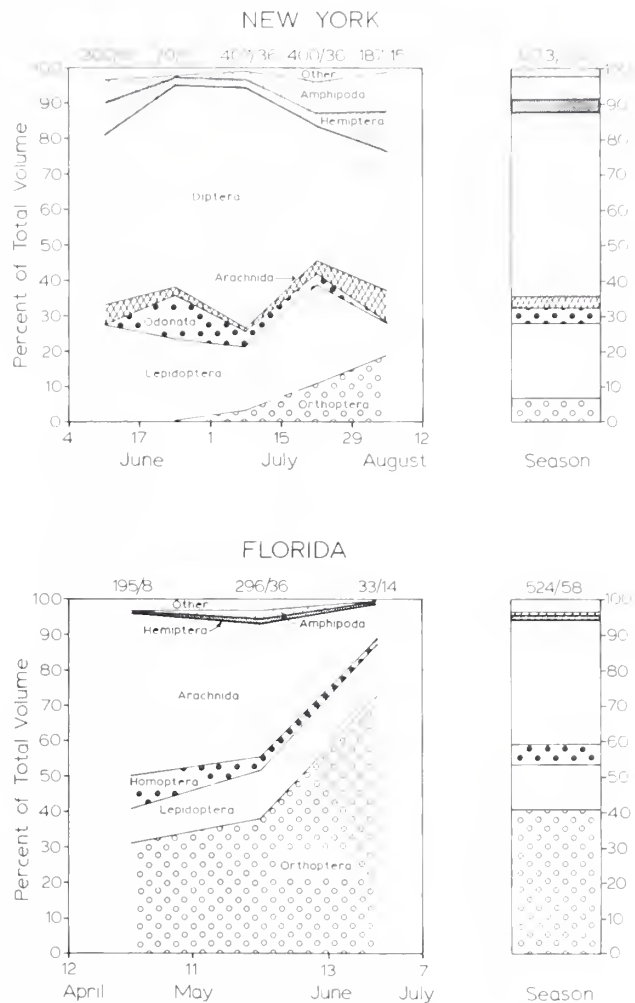
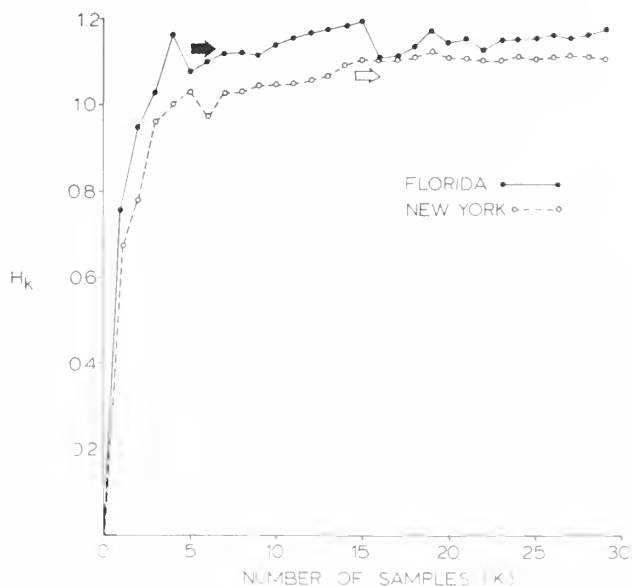


Fig. 3. Seasonal changes in the use of invertebrates by nestling Seaside Sparrows (percent composition by volume). Upper graph is New York, lower is Florida. Graphs on the right summarize the food distribution among the various prey groups for the whole season. The numbers above the graph indicate the number of food items (numerator) and the number of food samples (denominator) each interval represents.



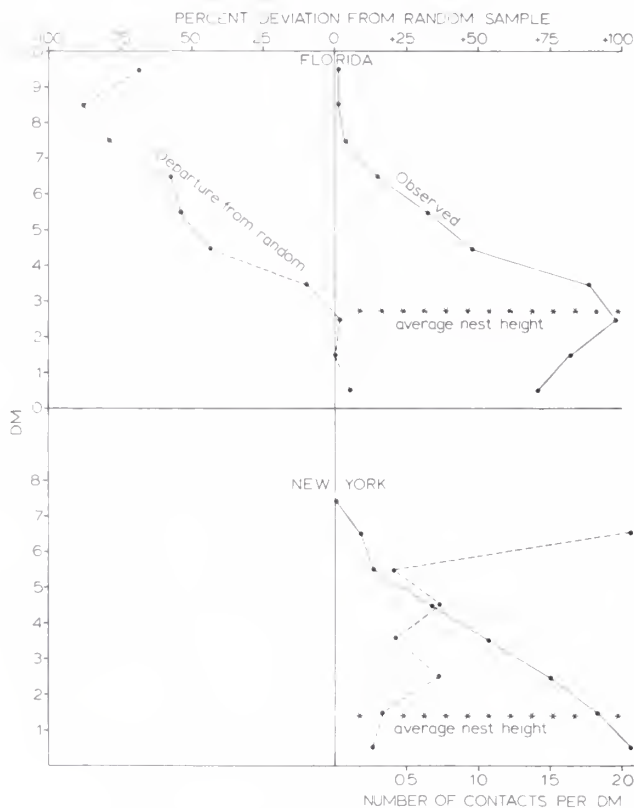


Fig. 5. Vegetation profiles of quadrats placed around Seaside Sparrow nests in New York and Florida. The lower abscissa indicates number of contacts that vegetation made with each dm interval on the measuring rod. The upper abscissa indicates the percentage of departure of the vegetation profile for each dm from the vegetation profiles of randomly positioned quadrats (Cody 1974). Ordinate labels the dm intervals for each area.

and associated chi-square (Table 3). To compare the power of the discriminant functions for New York and Florida, each case was examined *a posteriori* for correct group classification. Of the 270 quadrats in New York, 61% were correctly assigned. In Florida the discriminant function accurately predicted group membership for 74% of the 246 cases.

The relative contribution of each variable to group separation may be assessed by the sizes of the standardized discriminant function coefficients. In the Florida marsh the density of residual vegetation, followed by total vegetative density and by number of contacts at height of highest density, contributed most to discriminating nest sites from randomly chosen sites.

Comparing the vegetation profiles for each area further illustrates the greater divergence of Florida nest sites from the marsh as a whole (Fig. 5). This difference between the two populations may also reflect the greater vegetative uniformity of the northern marsh. However, in New York the closer correspondence of Seaside Sparrow nests to the general habitat pattern probably resulted from choice rather than from limited options, or from inadequacy of the discriminating variables. For example, using the same variables, we have found that the nest sites of Sharp-tailed Sparrows in the

same marsh diverged significantly from the habitat as a whole (unpubl. data).

The habitat selection picture is complicated by interactions with other species. In the southern site sparrows and Rice Rats competed for the same vertical space. Both species appeared to favor *Juncus* for nesting, as it provided the best protection from predators and also allowed them to put their nests high enough to avoid flooding. But Rice Rats were competitively superior to Seaside Sparrows, and seemed to exclude them from *Juncus* (Post 1981). Seaside Sparrows nested more often in *Distichlis* and *Salicornia*, where they were actually less successful (Fig. 6). For example, the probability of survival of 21 nests in *Salicornia* was 0.003 to 0.004 (95% confidence interval for the 21 days of the nest cycle), while 13 contemporaneous nests in *Juncus* had a survival probability of 0.010 to 0.341. Similarly, Seaside Sparrows in New York did not nest in *Phragmites*, although it seems that this reed would provide the most secure cover for nests. However, *Phragmites* is occupied by Long-billed Marsh Wrens, which puncture the eggs of other species (Picman 1977). In addition, New York nest failures, often caused by snakes and small mammals, significantly decreased with distance from the landward edge of the marsh. Sharp-tailed Sparrows, which use nest sites similar to those of Seaside Sparrows, nested closer to the marsh edge, but did not suffer increased predation as a result (unpubl. data). Another complication arises from the fact that the nest success of both *Ammodramus* species is related to distance to closest neighbor. This relationship probably results from the hunting behavior of predators like Fish Crows (*Corvus ossifragus*), which intensify their searching in a local area when they are rewarded with a meal (Tinbergen et al. 1967). For the Seaside Sparrows in New York, the average intraspecific distance between closest contemporaneous nests was 32.6 ± 1.3 m ($N = 184$), while the average distance between Seaside and Sharp-tailed Sparrow nests was 46.4 ± 2.4 m ($N = 184$). Male and female Seaside Sparrows consistently chase Sharp-tailed Sparrows that land near their nests. The aggressiveness that Seaside Sparrows show toward other species in their territories may be explained in part by advantages gained by individuals that increase the distance of neighbors that have similar nests.

Territory Size and Mating System

Territory (advertized and defended area) size in the Florida population averaged slightly larger than in New York (Table 4). This difference probably is not related to fewer resources in the southern marsh, but rather to greater availability of suitable habitat in relation to Seaside Sparrow productivity (see later).

In comparison to other areas, the New York and Florida populations studied here had smaller territories (Table 4). The larger territory sizes reported for other populations may be related to the lower density of Seaside Sparrows in marshes with reduced tidal flow, which is correlated with lower productivity of angiosperms (Niering and Warren 1980) and thus invertebrates (Bourn and Cottam 1950, Smalley 1959, Davis and Gray 1966).

In both northern and southern groups all pairs that we studied were monogamous. Females built the nest

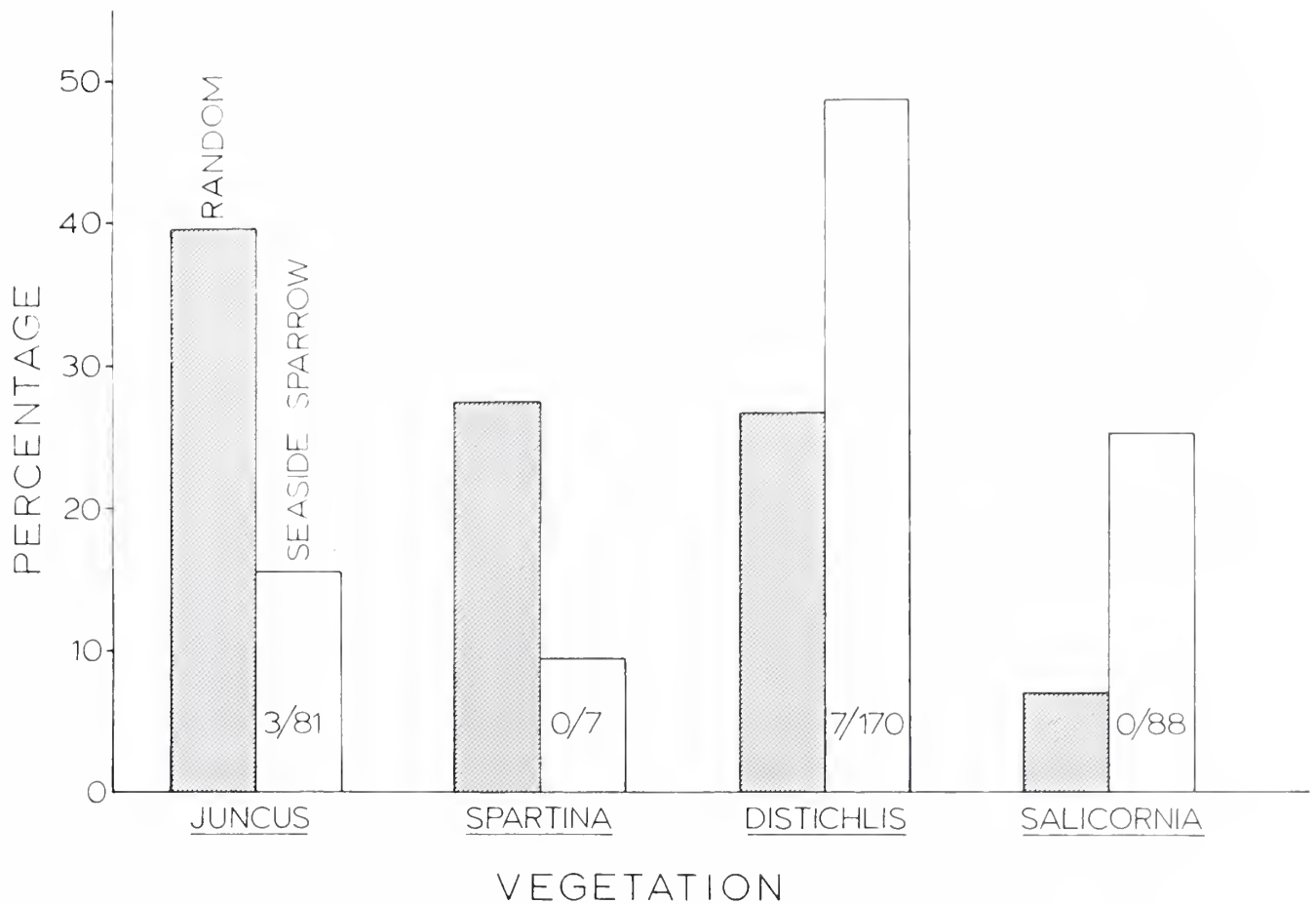


Fig. 6. Nest-site use of Seaside Sparrows in Florida. Shaded bars indicate percent availability of vegetation type; open bars indicate the percentage of Seaside Sparrow nests that were located in each vegetation type. Numbers in open bars are estimates of nest success (numerator: number of nests succeeding; denominator: number of days that nests were exposed to risk).

TABLE 4. Population densities and activity space sizes of Seaside Sparrows in various regions.

	Size of study area (ha)	Crude density (σ /ha)	Size (ha) of total activity space (AS)			Ecological density (σ /ha)= (1/AS)
			N	$\bar{x} \pm SE$	Range	
Florida (unaltered marshes)						
Gulf Hammock ¹	15.0	3.27	37	0.16+0.02	0.02-0.32	6.27
Taylor Slough ²	30.2	0.51	43	1.50	0.30-6.60	0.67
Ochopee ²	—	—	10	3.60	0.70-6.80	0.28
St. Johns ³	—	—	14	0.51	0.16-1.06	1.95
New York ⁴						
Oak Beach (unaltered)	2.8	20.00	25	0.12+0.02	0.02-0.62	8.31
Tobay (altered)	6.3	0.64	13	0.88+0.24	0.81-1.76	1.14
Louisiana (unaltered) ⁵	40.5	1.68	—	—	—	—
Maryland (unaltered) ⁶	7.9	0.25	—	—	—	—
New Jersey (altered) ⁷	7.8	1.02	—	—	—	—
North Carolina (unaltered) ⁸	19.0	1.70	—	—	—	—

¹ Present study.

² Werner 1975.

³ Baker 1973.

⁴ Post and Greenlaw 1975.

⁵ Norris 1968.

⁶ Springer and Stewart 1948.

⁷ Woolfenden 1956.

⁸ Quay 1953.

TABLE 5. Breeding productivity and replacement rates of Seaside Sparrows in New York and Florida.

Variable	NEW YORK		FLORIDA	
	1977	1978	1979	1980
Clutch size	3.70 \pm .57(N=56)	3.58 \pm .58(71)	3.08 \pm .31(78)	3.10 \pm .30(31)
Number of nests examined to determine success	64	82	34	43
Egg success, egg period (12 days) ¹	.5645	.5796	.0318	.1182
Egg success, nestling period (9 days) ¹	.5600	.6591	.1936	.4030
Egg success, 21-day period ¹	.3161	.3820	.0062	.0476
Daily nest mortality rate ²	.0300	.0363	.2302	.1579
Length of breeding season (days)	83.65	66.67	102.80	88.57
Number of young/♀/year ²	4.30	4.17	0.17	0.99
Replacement rate (R ₀)	2.76	2.68	0.33	1.89

¹ Calculated by methods of Mayfield (1975) and Johnson (1979).

² Calculated by method of Ricklefs and Bloom (1977).

without male aid, and incubated and brooded the young alone. Males, however, fed the young as often as the females did, usually starting on the day after hatching. In both the northern and southern groups, males and females delivered food at the same rates. The delivery rates per young per hour were also the same between geographic areas. The delivery rates per young per hour by New York females was $2.00 \pm (\text{SE}) 0.82$ ($N = 30$ h). The comparable value for Florida females was 1.69 ± 0.16 (21). The male delivery rate in New York was 2.08 ± 0.55 (30); in Florida, 1.32 ± 0.18 (21). In both regions males and females frequently left their nesting territories to gather food for their young, a behavior described previously (Post 1974).

During 1977 and 1978 in New York, we discovered no males that were not mated at some time during the breeding season. In Florida, however, a number of birds, probably first-year males, remained unmated through the breeding season. The number of bachelor males in the population varied between areas of the study site. In 1980 the western half had a larger proportion of unmated males (23% of 22) than the eastern (11% of 18). This difference was probably related to the less suitable habitat in the western half, reflected in the lower density of Seaside Sparrows there. These differences, in turn, were related to the greater area of short vegetation, and probably to lower rates of predation by rodents in the eastern half. The differences in numbers of unmated males between the two sections of the Florida site is analogous to differences existing between populations occupying altered and unaltered marshes in New York. In 1970 in a ditched salt marsh 12 km from Oak Beach, where Seaside Sparrow density was 1 male per ha, only 40% of the males had mates (Post 1970b). At Oak Beach during the same period, male Seaside Sparrow density averaged 8/ha, and all males were mated (Post 1970a).

Breeding Success and Productivity

The probabilities of survival of Florida nests were lower than New York nests in both years. For the 2 years in New York, the average Seaside Sparrow egg had a 35% chance of becoming a fledgling, whereas in

Florida over 2 years only 3% of the eggs produced fledglings (Table 5). Within any year on both sites, we found no differences between the daily survival rates of eggs (at risk for 12 days) and nestlings (9 days). In Florida the probability of egg success over the 21 days was significantly lower in 1979 than in 1980. This difference was mainly attributable to Rice Rat predation during the egg period.

The patterns of mortality between the two sites were different. At the northern site, proportionately more young and eggs succumbed to floods and rains associated with storms. In contrast, weather-related mortality was less important in the southern marsh. Predators, mainly Rice Rats, destroyed most nests in Florida: for the 2 years, 30% of the losses of young and eggs could be assigned to this cause. The 30% figure is undoubtedly low because many of the nests in the "unknown predator" category were probably destroyed by Rice Rats also (Fig. 7). Rice Rats took proportionally more eggs than young, whereas in New York, where Rice Rats were absent, and where Norway Rats (*Rattus norvegicus*) were the main mammalian predators, more nestlings were taken.

Productivity, the number of fledglings/female/year, is calculated by the method of Ricklefs and Bloom (1977). In this calculation for New York, the interval between renesting and nest failure is 5.5 days, and in Florida, 7.8 days. The interval between fledging and initiation of a new clutch is 17.5 days in New York. Lacking data for Florida, we used the latter estimate there also.

Although Seaside Sparrows in Florida had on the average a breeding period 21 days longer than those in New York, this difference failed to compensate for their significantly lower clutch size and breeding success (Table 5). Our productivity estimates for the 2 years combined indicate that female Seaside Sparrows in New York produced about seven times as many young per season as did those in the Florida marsh.

Survival and Population Maintenance

In New York the annual survival estimates are based on the cumulative return rates (Custer and Pitelka

1977) of residents banded from 1967 through 1972 and recaptured or resighted through 1980. The results of this analysis (Post and Greenlaw 1982) give estimates of adult survival of 57 to 60%, while individuals banded as nestlings or fledglings had a return rate of about 51%. As in other estimates of this kind, these are minimum values, as some individuals may have emigrated.

Our Florida data are incomplete, and we have survival estimates only for adult males. Of 21 males whose activity spaces were mapped in spring 1979, 18 survived into the breeding season of 1980, giving a minimum return rate of 85.7%. This figure is probably realistic, as it is close to the 88% estimate that Werner (1975) made for adult males in another Seaside Sparrow population in Florida.

To compute the replacement rates of the two populations, we assume that (1) the secondary sex ratio is equal, and as male and female fledglings are the same size, we have no reason to believe this is not the case (Fisher 1930); (2) in Florida, as in New York, the survival rates of adult females and males are about the same; (3) in Florida the ratio of juvenile female survival to adult female survival is the same as in New York, i.e., $51.43/60.36 = 0.85$; and (4) adult survival rates are constant over time.

In Florida the replacement rate averaged 1.11 over the 2 years, while the corresponding value for the New York population was 2.72 (Table 5). These results, then, indicate that over the 2 years of the study the Florida population was maintaining itself, whereas the New York population was increasing.

DISCUSSION

The populations of Seaside Sparrow studied here, situated near the opposite extremes of the species' latitudinal range, showed more similarities than differences in their responses to their salt-marsh habitats. In both areas Seaside Sparrows foraged on the ground, usually in *S. alterniflora*. They obtained most food by gleaning vegetation. In contrast to Florida birds, those in New York captured proportionally more food by probing or gleaning the mud, mainly to obtain immature flies. Florida birds seldom fed by this method, because of the few insects in the mud. Seaside Sparrows in the southern marsh fed more in the herb layer, taking proportionally more moths and grasshoppers than did northern birds. In spite of the greater arthropod diversity of the Florida marsh, sparrows at this site exhibited about the same degree of diet specialization as New York birds. In both areas a few groups of arthropods composed the bulk of the nestling diets.

The differences in patterns of food availability and use that we found between New York and Florida parallel those that Orians (1973) found for Red-winged Blackbirds nesting in Washington and Costa Rican marshes. In Washington, as in New York, the marsh-dwelling birds took greater numbers of insects with aquatic stages in their life histories. In Costa Rica and in Florida, herbivorous insects increased in importance. These differences in both studies appear to be related to availability of insects, rather than to preferences of birds. In Costa Rica the emergence of dragonflies, which were the most commonly taken food in Washington, was impeded by dense mats of grass. Costa Rican black-

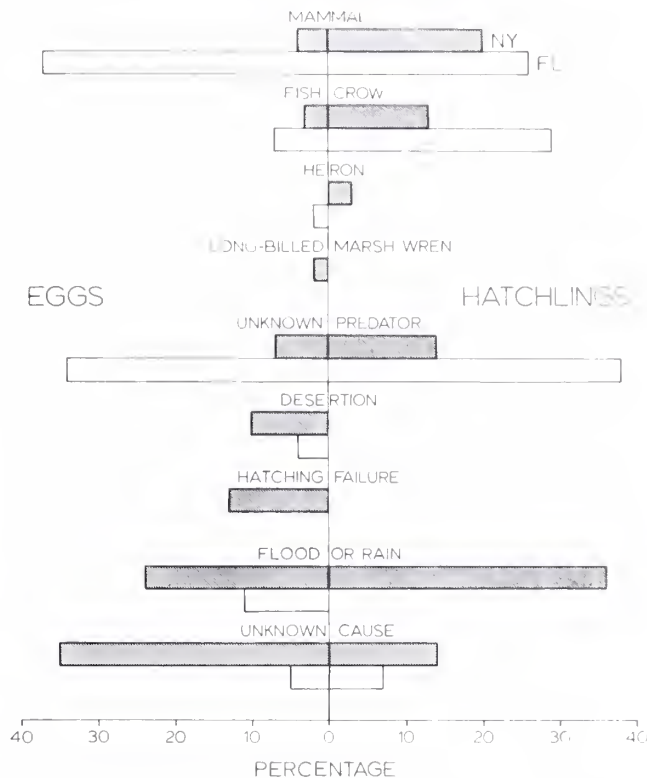


Fig. 7. Comparison of causes of nest mortality in New York and Florida. Solid bar = New York; open bar = Florida. Sample sizes: New York, 136 nests with eggs, 127 with young; Florida, 161 and 42.

birds caught mainly orthopterans and lepidopterans, as did Seaside Sparrows in Florida. Although Odonata are uncommon in salt marshes, flies are usually abundant, and were taken often in New York. However, flies were uncommon in the Florida marsh, probably because of the competition that their immatures encountered with mud-inhabiting saprovores. Orians (1973) also found few flies taken by Costa Rican blackbirds, but did not explain their scarcity.

During the period of the study, we doubt that Seaside Sparrow reproductive capacity was affected by food availability. First, in the southern salt marsh, arthropods were available throughout the year. Early in the nesting season Seaside Sparrows used a greater proportion of spiders. As the season progressed, proportionally more grasshoppers were taken. If one group of invertebrates was depleted, foraging birds could have switched to alternate sources, some of which, like crabs or polychaete worms, are marine. Second, many terrestrial organisms taken by Seaside Sparrows are adults with aquatic immature stages. Such food sources are rapidly replenished (Orians and Horn 1969). Third, many invertebrates that consume *Spartina* immigrate from other areas (Kale 1965), compensating for any local depletion. Fourth, the population studied in Florida did not compete with other birds for food during the nesting season. No other small birds nested in the study area. The sparrows' main competitors for insects were spiders, which were a food source for the sparrows. During the winter the density of small birds in the study area increased by 10-fold (unpubl. data). Even then it is doubtful that food was limited. In addition to

the large amounts of seeds (primarily *Distichlis* and *Spartina*) available, arthropods, particularly Homoptera, were still abundant in midwinter. In essence, then, Seaside Sparrows in Florida use a buffered food supply throughout the year.

The same pattern of food abundance was apparent in the northern marsh in the summer. At this site only one other songbird, the Sharp-tailed Sparrow, fed in the same areas as Seasides. The diets of these two species overlapped broadly (Post and Greenlaw 1982), an indication that food was not limited for either. Female Seasides that had their mates removed were able to compensate for lack of male aid, and their nestlings did not lose weight (unpubl. data).

Both northern and southern Seaside Sparrows had limited nest-site options. In New York the size of appropriate nesting areas varied from year to year, as a result of winter storms. Moreover, tides and aerial predators probably restricted nesting birds to a narrow vertical zone of the grass. In Florida, horizontal availability of nesting habitat was relatively constant, but vertical sites were still limited. However, sparrows appeared to shift from densely vegetated to sparsely vegetated areas as a result of interactions with Rice Rats. Because of the different selection pressures in the two geographic areas, nest-site characteristics were different. Northern birds tended to use vegetation that was as dense as or denser than that encountered in the whole marsh. Southern birds selected nesting sites that were less dense than found in the rest of the marsh.

The reproductive success of the two populations differed. Although this was a short-term study, and greater fluctuations in success might be expected over a longer period (Wiens 1977), the large gap between the two groups (3% of the eggs produced young in Florida, compared to 35% in New York) probably would not be narrowed much by variations over time. The northern population suffered more mortality from catastrophic flooding than did the southern group. In the northern marshes predation was a less important mortality factor than flooding. Rice Rats are absent in New York, and predation by rodents was relatively uncommon. The most important predators were Fish Crows and Marsh Hawks (*Circus cyaneus*). The main factor accounting for the very different breeding success in the two areas seems to be the presence of Rice Rats in Florida. High incidence of Rice Rat predation has been seen in other southern marshes (Kale 1965, Orians 1973, Wiley and Wiley 1980). In Georgia salt marshes Kale (1965) found that Long-billed Marsh Wren nests often were attacked by Rice Rats: in 1959, 84% of egg and nestling losses were attributed to Rice Rats. The low number of bird species nesting in southern salt marshes may be related to the presence of Rice Rats. At the Florida site eight species of songbirds were common in the winter, but only Seaside Sparrows remained to breed.

The Seaside Sparrow pairs at both sites defended nest-centered activity spaces. As in other littoral populations that have been studied (Woelfenden 1956, Post 1974), the degree to which these areas were used for foraging probably depended on their size, and on the quality of the feeding areas within the limits of the territories. Activity spaces often overlapped, and both sexes

left the defended territory to forage, often long distances from the nest. In contrast, Seaside Sparrows in nontidal marshes and in altered salt marshes occupied significantly larger territories and apparently carried out all activities within their confines, although territory borders fluctuated and overlap of adjacent spaces occurred (Post 1974, Werner 1975).

More than determining local population density, the space-use patterns of Seaside Sparrows appeared to be determined by the number of birds attempting to settle in an area. As population density increased, territory size decreased, and individuals spent more time feeding away from their territories (Post 1974). As in other passerines whose foraging behavior has been studied during the nesting period (Hussell 1972), parents foraging for nestlings tended to fly long distances from the nest, often ignoring territorial boundaries.

A number of studies of the use of space by small birds suggest that few males actually defend areas for their food value *per se* (Waser and Wiley 1979). Males probably advertise and defend fixed sites in order to increase their chances of mating, and once mated, as a means of limiting access to females. The availability of food within the defended area is only one of the features used by females in assessing territory quality. Individuals occupying habitat islands, in which suitable foraging sites are limited (Post 1974, Knapton 1979), may forage more off territory than on. Further, grouping of territories (Post 1974) and off-territory foraging behavior give the appearance that these populations are colonial, in sense of social affiliation. The use of the term "colony" is misleading, and the literature contains many references to colonies of Seaside Sparrows (cf. Austin, this symposium). A distinction should be made between aggregation motivated by a common response to habitat features or by social attraction, although this may be difficult in practice, for both motivations may be involved simultaneously.

Throughout its range the Seaside Sparrow is opportunistic, though severely constrained by a temporally heterogeneous (Menge and Sutherland 1976) environment. Its life style has these salient features in common between regions: (1) diverse feeding behavior, which reflects behavioral flexibility as well as superabundance of food (Wiens and Rotenberry 1979, Rotenberry 1980); (2) a pattern of monogamy and of nest-centered aggressivity by both sexes that does not vary between regions; and (3) variability in habitat selection behavior (cf. Austin, this symposium). However, the close correspondence of the nest-site characteristics of the populations studied here reveals that on the average this niche dimension is quite narrow. Convergence in habitat selection over a wide geographic area results from the structural simplicity of the vegetation and is accentuated by interactions with competitors. As Seaside Sparrow territory sizes do not vary predictably with resource availability (unpubl. data), monogamy may be viewed as the conservative response of a species occupying an unpredictable habitat. Also, territoriality, to the extent that it leads to spacing-out of nests, may be advantageous in a species subjected to intense predation. Thus, monogamy and female aggressivity, through their association with territoriality, are selected for throughout the species' range.

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PART III
Protection and Management
of
Seaside Sparrow Populations

Habitat Use and the Distribution of the Cape Sable Sparrow

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Dedication. We dedicate this paper to the late Louis A. Stimson, whose endurance and perseverance in searching for Cape Sable Sparrows contributed so much to our knowledge.

The Cape Sable Sparrow (*Ammospiza maritima mirabilis*), a subspecies of the Seaside Sparrow endemic to extreme southern Florida, has elicited considerable interest and concern since its discovery in the early 1900s. Before being relegated to subspecific status (Eisenmann 1973), it was considered to be the last bird species described from the continental United States (Howell 1919, Stimson 1968). The sparrows were widely believed to have been exterminated from Cape Sable by a hurricane in September 1935 and were not rediscovered there for 35 years (Werner 1971).

The limited distribution, and apparently catastrophic history, of the Cape Sable Sparrow resulted in its being classified as endangered under the original Federal listing of endangered species in 1967. Discoveries, apparent losses, and rediscoveries of sparrow populations in various areas have characterized its known history. One cause of its being little understood is the habitat it occupies. Unlike other races, which are confined to coastal salt marshes, the Cape Sable Sparrow occurs predominantly in inland freshwater marshes. Such unexpected choice of habitat made it less likely for such populations to be discovered, and as a result, the status and distribution of the sparrow have remained poorly known. In an attempt to characterize the distribution and habitat use of the Cape Sable Sparrow, we undertook extensive surveys from 1978 to 1980, and a census covering all available habitat in 1981. As a result, we have found that the sparrow is much more widely distributed than was previously thought. In this paper we document the present range of the Cape Sable Sparrow, characterize its use of habitat, and provide an estimate of its population size.

METHODS

Surveys were conducted in known and suspected Seaside Sparrow habitat in extreme southern Florida, primarily south of US 41 (Fig. 1). Urban and agricultural areas were excluded. Like Werner (1975), we found during this study that sparrows do not use habitat containing trees or brush. As a result, the extensive mangrove, pine, and cypress forests of southern Florida are unsuitable as habitat. Sparrows also do not occur in deeply flooded marshes such as the Sawgrass-dominated areas of the Everglades proper. The typical Seaside Sparrow habitat of cordgrass (salt) marsh occurs along the coast embedded in and on the edge of mangrove forest (Fig. 1). Our census, therefore, covered all of the treeless coastal and inland freshwater marshes and prairies of extreme southern Florida, except the deeper marshes of Shark River Slough, the central core of the Everglades (Fig. 1).

Preliminary surveys were conducted from early April through late June, 1978-1980. We covered easily accessible areas on foot. More remote areas where sparrows had been previously observed and other potential habitat were surveyed using a Bell C-47 helicopter equipped with pontoons. We began our flights at approximately sunrise and continued for 3 to 4 hours. To census a site, we landed and shut off the engine. While walking around the aircraft for about 10 minutes, we listened for singing sparrows. When a singing bird was detected, we moved near and recorded the number of birds seen or heard. In these preliminary surveys, small patches of habitat were covered thoroughly; whereas, in large areas of suitable habitat, we surveyed selected sites several kilometers apart. One

to 10 sites were surveyed each morning. In 1981, we censused all potential habitat systematically from 31 March through 16 June. All potential habitat was gridded into blocks 1 km on the side, which were plotted on U.S. Geological Survey 7.5-minute orthophoto quadrangles. We conducted our census at the intersection of the grid lines. The number of birds seen or heard and characteristics of the plant community were recorded. The exact locations of the survey sites and habitat information are provided in Bass and Kushlan (1982).

At each census location, we were able to hear a sparrow within 200 m. We believe we censused singing birds within an area of 12.6 ha around the helicopter landing point. The number of birds observed in the 12.6 ha-plot represents the minimum number of singing males there, and the density in the plot is taken to be representative of the density of singing males in the adjacent 1 km² block. We obtained a population estimate by multiplying the average density of birds per km² by the number of occupied square kilometers, then doubled the number to include uncounted females.

We characterized the habitat in each plot according to its dominant plant cover. Freshwater prairies and marshes included Muhly prairie, mixed prairie, cordgrass marsh, Sawgrass marsh, Cat-tail marsh, and Black Needlerush marsh. Forest communities included mangrove swamp forest, cypress swamp forest, pine forest, and hammock forest. In nearly all cases, we found sparrows only in the first three plant communities listed. Werner and Woolfenden (this symposium) recognize four habitats: clumped cordgrass prairie, unclumped cordgrass prairie, sparse Sawgrass prairie, and Muhly prairie. Our classification for this paper combines their two cordgrass habitats. Their sparse Sawgrass community is equivalent to our mixed prairie.

Muhly prairie is a mixture of grasses, sedges, and forbs in which graminoids predominate. This community occurs on marl soil and has a short (1 to 6 months) hydroperiod. Muhly (*Muhlenbergia filipes*), a bunchgrass, dominates plant community structure in frequency and cover (Olmsted et al. 1980). In some areas Black-top Sedge (*Schoenus nigricans*) is the dominant clumped species, and Muhly is secondary. The bunchgrasses are 60 to 90 cm high. Sawgrass (*Cladium jamaicense*) is a constant associate and is usually 20 to 30 cm taller than Muhly or Black-top Sedge. *Schizachyrium rhizomatum* and *Rhynchospora* sp. also occur. Overall, the community may contain up to 20 species of graminoids and 50 species of forbs. Graminoids make up 98% of plant cover, which varies with hydroperiod, soil depth, and fire history. Large areas of Muhly prairie have sparse, 10 to 25%, cover (Olmsted et al. 1980).

Except for lacking Muhly, mixed prairie is similar in composition to the Muhly prairie. The absence of Muhly changes the structure of the community, by eliminating the grassy clumps. A greater mixture of species includes *Rhynchospora* sp. and grasses, especially *Panicum virgatum*. Sawgrass is always present.

The remaining marsh communities are dominated by their indicator species. Cordgrass marsh is composed primarily of *Spartina bakeri*. Sawgrass marsh has a longer hydroperiod than the prairie communities and occupies the central, deeper-water cores of the

southern Everglades, Shark River Slough, and Taylor Slough (Fig. 1). Cat-tail marsh is dominated by *Typha* sp., up to 3 m tall. Black Needlerush marsh, dominated by *Juncus roemerianus*, occurs within and near the coastal mangrove swamps in inland, nontidal situations.

Mangrove forest swamps are dominated by *Rhizophora mangle*, *Avicennia germinans*, or *Laguncularia racemosa*. Cypress swamp has *Taxodium distichum* as its dominant overstory tree. Big Cypress Swamp, northwest of Shark River Slough, comprises cypress swamp and pine forests of *Pinus elliottii*. Pine forests and hammock forests of tropical hardwoods form the remaining upland complex of plant communities of southern Florida. Much of the area naturally occupied by these communities has been subjected to agricultural and urban development.

RESULTS

History of Known Distribution

The Cape Sable Sparrow was discovered by A. H. Howell in 1918 on the coastal prairie of Cape Sable, at the southwest tip of the Florida peninsula (Howell 1919). The sparrow was found to range along much of the coast west of Flamingo (Fig. 1) (Stimson 1956, Werner 1971). Although Howell (1919) found that sparrows were only "moderately numerous," they were rather widely distributed in the prairies inland from the beach. The population survived the hurricane of 1929 (Howell 1932), but it was widely thought (Nicholson 1938; Stimson 1956, 1968) to have been extirpated by the hurricane of September 1935, despite observations to the contrary (Semple 1936, Dietrich 1938). Burleigh (1939) did not find them on a search in the winter of 1938.

When first discovered, the sparrow occupied seasonally flooded prairie, dominated by short, sparse cordgrass, *Distichlis spicata*, and *Sesuvium portulacastrum* (Holt and Sutton 1926, Semple 1936, Nicholson 1928, Stimson 1954, Werner 1978). Comparison of early descriptions and photographs (Holt and Sutton 1926) with current conditions shows that this area, once occupied by extensive cordgrass marsh, is now dominated by mangroves, bare mud flats, and stands of halophytic forbs (*Batis maritima*, *S. portulacastrum*, *Borrchia frutescens*). The plant community change was initiated by the hurricane of 1935 and resulted in a marked decrease of potential sparrow habitat on Cape Sable. Stimson (1956) searched for and failed to find sparrows there in 1949. Werner and Woolfenden (this symposium) suggest that by the time of that survey most of the habitat may no longer have been suitable for the sparrow. In 1970 Werner (1971) rediscovered sparrows on Cape Sable in several small residual interior stands of cordgrass marsh. At that time, Werner found four singing males and netted five juveniles in a 2-day effort. In much more limited surveys in 1975, one male was found (Werner 1975).

Cape Sable Sparrows were discovered west of the true Everglades (Shark River Slough) in the southeastern Big Cypress Swamp in 1928 (Nicholson 1928). They were separated from the occupied area on Cape Sable by bays and mainland mangrove forests. An error in reporting the location of these observations, later corrected by Stimson (1954, 1956), prevented immediate

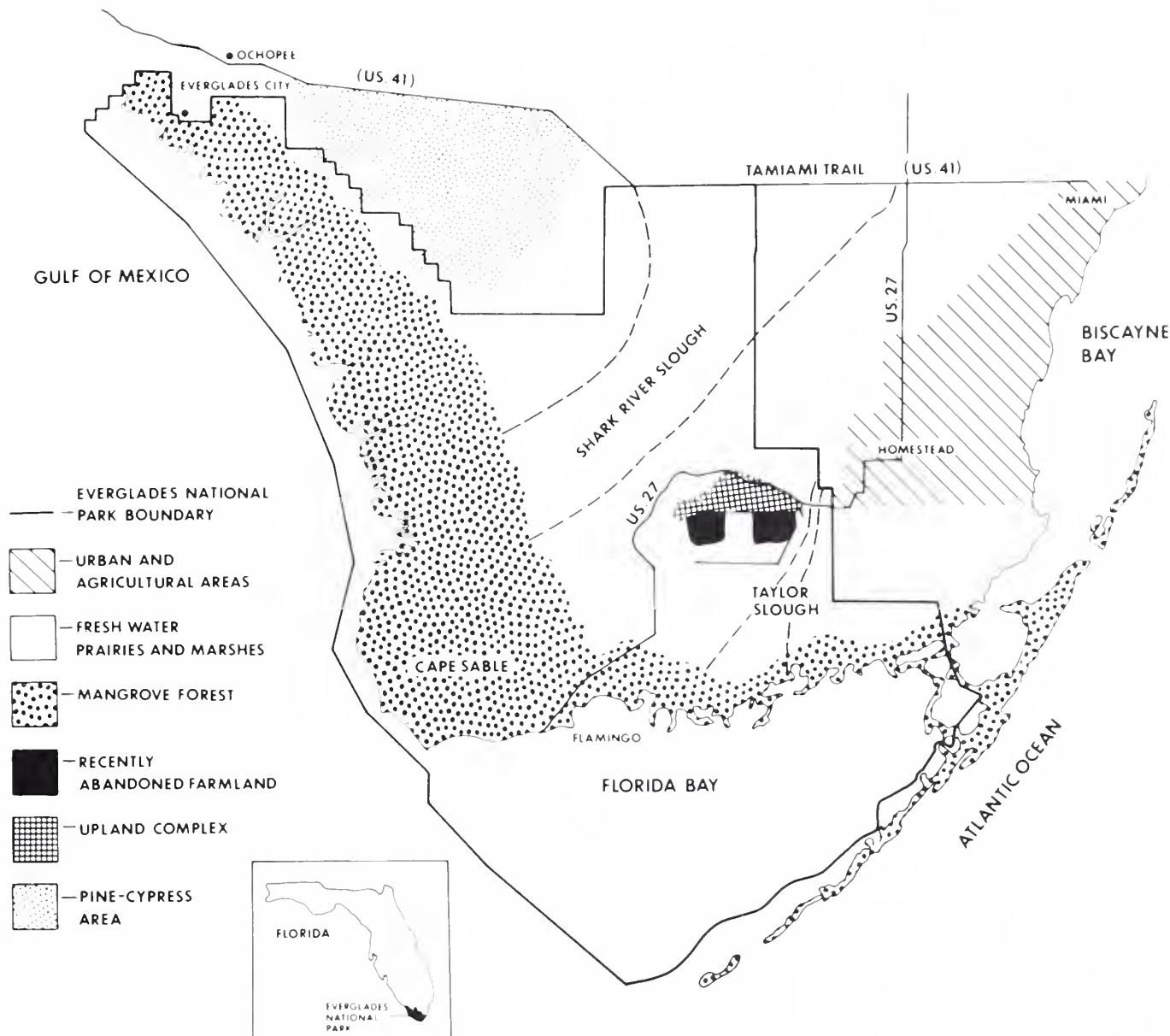


Fig. 1. Map of extreme southern Florida, showing localities, major plant communities, and physiographic areas.

confirmation of this discovery. Our knowledge of the distribution of sparrows in this area during the 1950s resulted from the work of Stimson and his colleagues (Stimson 1956 and references therein). He found that the sparrows were widely distributed as far east as the western edge of the southern Everglades. However, by the early 1960s, he (Stimson 1968) concluded that the population had been extirpated by widespread and frequent fires. Birds were found in the area in surveys conducted from 1970 to 1975, but Werner and Woolfenden (this symposium) concluded that they were rare at that time.

Sparrows were found in coastal marshes near Ochopee in 1942 (Anderson 1942). By the mid-1950s, Stimson (1956) determined that the birds were dispersed south of Ochopee in marshes between the mangrove swamps and cypress swamps. He reported a hiatus in distribution between these sparrows and those in the southern Big Cypress Swamp. In recent decades the habitat in these marshes has been changing. From 1970

to 1975, it appeared to Werner (1975) that *Juncus roemerianus* and *Eleocharis* sp. were replacing *Spartina bakeri* and *Distichlis spicata*. Mangroves also have shown a long-term encroachment inland, although this invasion may have been checked by freezes in 1977. Some of these changes were probably associated with altered hydrologic conditions in the area and with a high frequency of fires. Werner (1975) found sparrows at six scattered sites in this area from 1970 through 1975 and noted a decline in both the number of sites and number of individuals seen during the course of his study.

Sparrows were reported east of the true Everglades in Taylor Slough in 1972 (Ogden 1972). These birds occupy the prairie west of Homestead, north into the East Everglades, and southwest in Taylor Slough to the mangroves (Fig. 1). Werner (1975) found this population to be patchily distributed over an area of about 10,000 ha. The sparrow apparently existed in this area before its official discovery, as a previously overlooked



Fig. 2. Known distribution of the Cape Sable Sparrow from 1970 through 1975. Locations where sparrows were found by Werner (1975) are indicated by dots.

observation occurred in 1957 (Werner and Woolfenden, this symposium). Based on his surveys in 1974 and 1975, Werner concluded that this area supported most of the remaining sparrow population. Using information on sparrow density from his study plots, he estimated the population there to be between 1,900 and 2,800 birds (Werner 1978).

In the early 1970s, therefore, Werner (1975) had found that the sparrow persisted in each of the areas where it had previously been known to exist, but that very few individuals remained at Ochopee, on Cape Sable, or in the southern Big Cypress Swamp. Birds near Ochopee were undergoing a decline, whereas birds on Cape Sable were confined to small patches of remnant cordgrass marsh. The largest population was the newly discovered one near Taylor Slough. Figure 2 summarizes the sparrow's known range at the end of Werner's study.

Combining Werner's information with that of earlier workers, we can estimate the maximum known historic range of the Cape Sable Sparrow from 1918 through 1975 (Fig. 3). As discussed above, it appears that not all areas were occupied simultaneously, nor was each area densely occupied throughout the historical period.

Censuses of 1978-1981

In our preliminary censuses conducted from 1978 through 1980, we attempted to determine the location and status of persisting populations (Fig. 4, 5, 6). Details of the results are provided in Bass and Kushlan (1982). In 1978, censusing places where Werner had last found birds, we heard or saw birds at two sites on Cape Sable, at one site near Ochopee, and at 11 of 12 sites surveyed

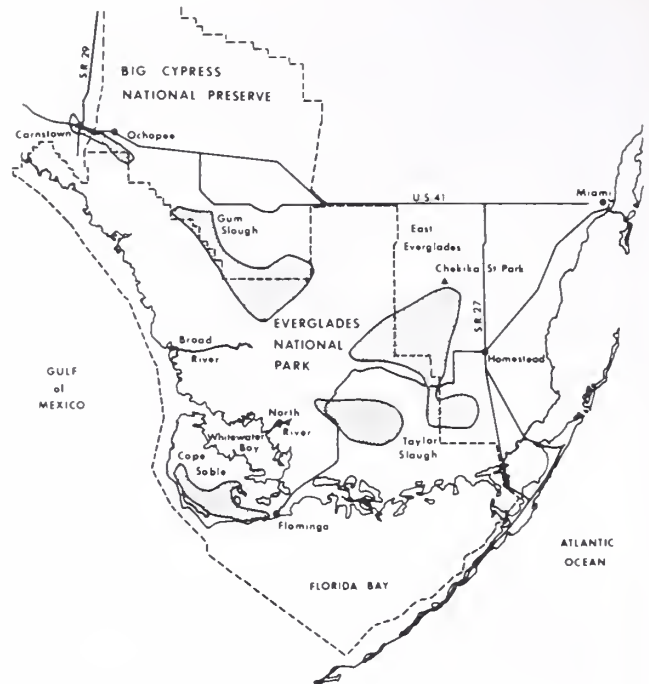


Fig. 3. Maximum extent of the known range of Cape Sable Sparrows, 1918 through 1975. The sparrow was probably absent from some of these areas through some or most of the period.

in Taylor Slough. In 1979, we were unable to find birds in their previous locations on Cape Sable, because most of that habitat had burned that year. We found birds at two sites near Ochopee and in 11 of 20 sites surveyed near Taylor Slough. In 1980, we were unable to find birds on Cape Sable or near Ochopee. A more extensive survey in the Big Cypress Swamp uncovered birds at 12 of 21 sites. We also found sparrows at 32 of 50 sites censused near Taylor Slough.

This 3-year survey period demonstrated a continued retraction of sparrow distribution from that of 1975 at Ochopee and at Cape Sable, with birds not being found at these sites in the last year of the survey. However, the rediscovery of a large and well-dispersed population west of Shark River Slough and expansion of the known distribution of sparrows near Taylor Slough suggested that a substantial total population remained. To determine precisely the distribution of the remaining birds, censuses were made 1 km apart throughout the known or otherwise suitable range. All prairie habitat was surveyed along with adjacent marginal habitat dominated by Sawgrass, cypress trees, mangrove trees, or hammocks.

The results show that, as of 1981, the Cape Sable Sparrow was widely distributed over large areas of southern Florida west and east of Shark River Slough (Fig. 7). The location of all spots censused and the data obtained at each are given in Bass and Kushlan (1982). Overall, 864 locations representing 864 km² were censused (Table 1). We found 278 or 32% of these locations to be occupied by Cape Sable Sparrows. Sparrows therefore occurred over 27,800 ha.

The census results for each of four subpopulations are shown in Table 1. We saw no sparrows at five sites

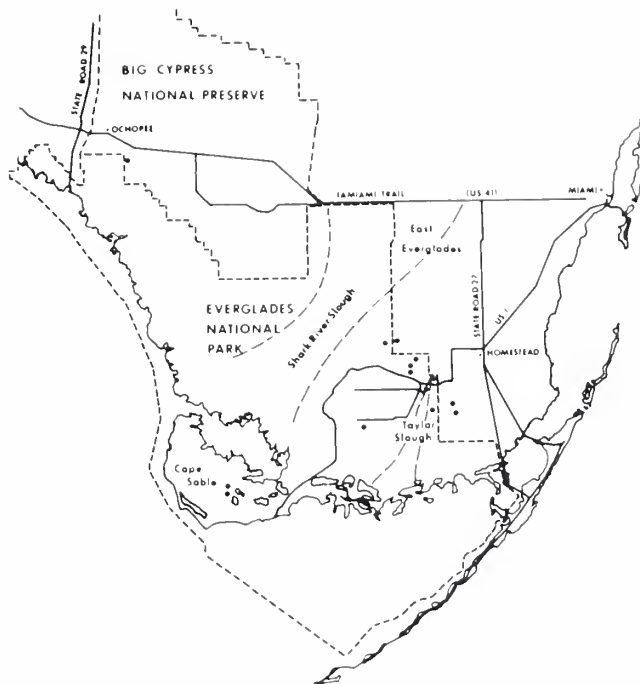


Fig. 4. Locations where Cape Sable Sparrows were found in 1978.



Fig. 5. Locations where Cape Sable Sparrows were found in 1979.

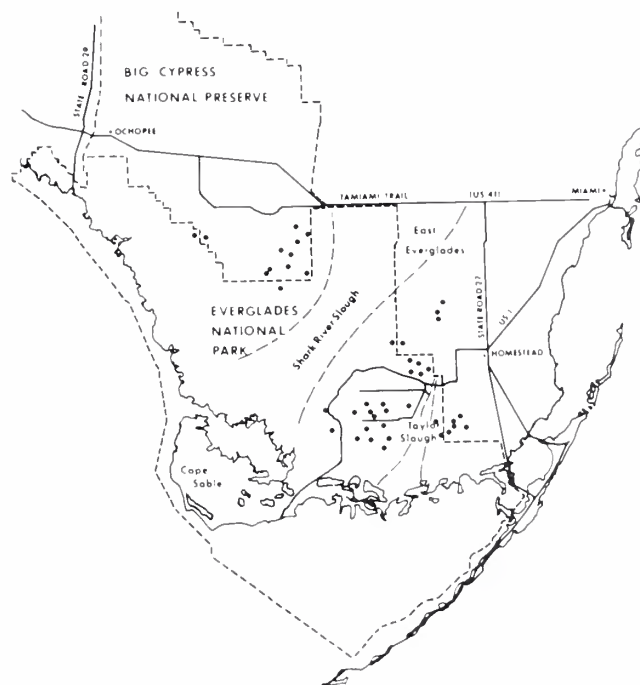


Fig. 6. Locations where Cape Sable Sparrows were found in 1980.

on Cape Sable, representing total coverage of all available habitat there. Similarly, we found no birds near Ochopee. In Taylor Slough and the southern Big Cypress Swamp, however, we counted over 400 birds at the 278 sites. Of the 396 plots surveyed near Taylor Slough, 39%

were occupied by sparrows. The high percentage of occupied census plots reflects the clear demarcation between suitable prairie habitat and the surrounding unsuitable habitats of tall Sawgrass marsh, pine forest, mangrove forest, hammock forest, or developed land, which we did not census. As a result, the periphery of the census area was well defined, and most of our census plots were in suitable habitat. The 28% occupancy of the Big Cypress area was due to the complex interdigitation of marginally unsuitable habitats and isolated patches of prairie habitat that required censusing. The habitat in the two large areas occupied by sparrows is probably grossly equivalent because the number of birds per occupied site was similar.

Habitat Use

During the 1981 census, we also determined characteristics of the habitat used by Cape Sable Sparrows. Most birds occurred in habitat dominated by the grass, *Muhlenbergia*, and 67% of the occupied habitat was Muhly prairie (Table 2). Muhly and the similar mixed prairie together accounted for 96% of the habitat occupied by sparrows. Furthermore, half of all Muhly and mixed prairie habitats surveyed, which included essentially all of that available in the study area, supported sparrows. We also found sparrows in 8 of 61 sites dominated by cordgrass and at two plots that contained cypress trees.

It is conceivable that the value of habitat to sparrows could be indexed by the number of singing male birds seen per occupied site. Within the admittedly coarse resolution of this method, it does not appear that the occupied habitats were grossly dissimilar. The situation is more complicated than our census revealed, however, because Werner (1975) and Taylor (this symposium) found differences in density of breeding birds related to the sites' fire history.

TABLE 1. Cape Sable Sparrows found on censuses conducted in 1981 in four areas of southern Florida.

Subpopulation areas	Number of sites	Number of sites occupied	Number of birds seen	Percent of sites occupied	Birds per site	Birds per occupied site
Taylor Slough	396	155	248	39	0.6	1.6
Big Cypress	441	123	168	28	0.4	1.4
Ochopee	22	0	0	0	0	0
Cape Sable	5	0	0	0	0	0
Totals	864	278	416	32	0.5	1.5

TABLE 2. Habitats occupied by Cape Sable Sparrows in 1981.

Habitat type	Number of sites	Number of sites occupied	Number of birds seen	Percent of sites occupied	Birds per site	Birds per occupied site
Muhly prairie	371 (43) ¹	186 (67) ²	290	50	0.8	1.6
Mixed prairie	164 (19)	82 (29)	111	50	0.7	1.4
Cordgrass marsh	61 (7)	8 (3)	12	13	0.2	1.5
Sawgrass marsh	175 (20)	0 (0)	0	0	0	0
Other	93 (11)	2 (1)	3	2	0.03	1.5

¹Percentage of total habitat surveyed.²Percentage of total habitat occupied.

Population Estimate

Using the area covered by each of our census plots, we estimate the population of adult Cape Sable Sparrows in 1981 to be 6,640, or rounded to 6,600. Werner (1976) had estimated that the Cape Sable Sparrow population in 1975 was between 2,000 and 3,000 birds. He arrived at this figure by extrapolating population densities within measured plots in Taylor Slough over the area of known occurrence. The range of estimates, set by extrapolating sparrow density on good and on poor plots, was 1,800 to 27,800 individuals. However, considering only the study site most typical of Taylor Slough as a whole, he estimated the population there to be 1,900 to 2,800 sparrows. Having found very few sparrows in areas other than Taylor Slough, he suggested that this subpopulation accounted for 95% of the population and thereby incremented his estimate slightly to account for other birds. Our data suggest that in 1981, the Taylor Slough population accounted for 3,700 sparrows. The primary difference between the two estimates of total population (3,000 vs 6,600) is in our addition of the Big Cypress subpopulation. Because we undoubtedly did not count all birds at each stop, we consider our estimate to be a minimum one. Thus we conclude that the Cape Sable Sparrow population seems to be in excess of 6,600 adults as of 1981.

DISCUSSION

Our census data suggest that the Cape Sable Sparrow has a larger population than previously thought. Over 6,600 birds are widely distributed over much of its

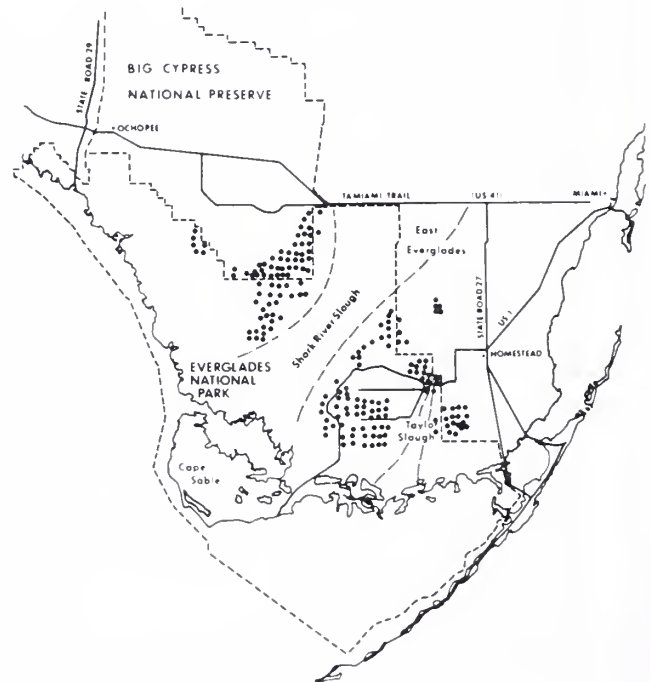


Fig. 7. Distribution of Cape Sable Sparrows based on censuses conducted in 1981. Suitable habitat was censused at locations 1 km apart. Because of the map scale, not all occupied sites are shown.

maximally occupied historic range (Fig. 3, 7). Despite this optimistic result, it is apparent that two subpopulations have been extirpated or at least reduced to very low numbers. These coastal populations, should they persist, are now marginal relative to the remaining population, which is concentrated in the extensive marsh prairies of inland southern Florida. The apparent loss of birds from Cape Sable seems primarily a natural phenomenon reflecting changes in the vegetation regime, whereas the loss of birds from the Ochopee area was probably man-caused by means of drainage and fires (Kushlan et al. 1982).

Current and future threats to the Cape Sable Sparrow seem to be habitat alteration from hurricanes, fire, drainage, and development. The nature of these threats and proposals for management are discussed in Kushlan et al. (1982). Hurricanes appear to have caused substantial, apparently irreversible, changes to some coastal habitat. Werner and Woolfenden (this symposium) concluded that the birds probably are able to survive the direct effect of hurricanes. Long-term habitat change, however, may have a devastating effect, as was demonstrated on Cape Sable. Too frequent or too severe fire, especially combined with drainage, can markedly affect sparrows. Werner (1975) and Taylor (this symposium) discuss the role of fire and its use as a management tool.

The greatest threat at present to an extant population is in the East Everglades, where loss of habitat is occurring due to drainage, frequent fires, invasion of exotic trees, and agricultural and urban development. Contraction of the population because of loss of habitat has rendered parts of the proclaimed critical habitat unsuitable for sparrows. This can be seen by comparing the critical habitat as of 1981 to present distribution of sparrows (Fig. 8) in the East Everglades. Should it be considered desirable to preserve that segment of the population, specific management is required to protect this habitat. Birds in the East Everglades have become an increasingly isolated and marginal group.

The apparent disappearance and reappearance of the Cape Sable Sparrow from known habitat is a matter of some interest. Much of the lack of information on the sparrow's historic distribution is undoubtedly a result of the difficulty in gaining access to much of the area. It also is related to the occurrence of the Cape Sable Sparrow over vast areas of freshwater marsh, where self-respecting Seaside Sparrows had not been expected to occur. However, we do not believe that all the reported disappearances are artifactual. We doubt that the birds were missed by Stimson (1956) on Cape Sable in 1949, by Werner (1975) in the Big Cypress in the early 1970s, or by Robertson (1955) in Taylor Slough in the early 1950s. Considering the dramatic effects of fire on habitat occupancy by sparrows (Werner 1975; Taylor, this symposium), it seems likely that fires covering large areas too frequently would render considerable habitat unsuitable. Reoccupancy would require a slow recolonization for this fairly sedentary bird. This conclusion suggests that unnatural fire must be controlled and used as a management tool in sparrow habitat (Kushlan et al. 1982; Taylor, this symposium) and that our population estimate may represent a high point in a fluctuating population cycle.

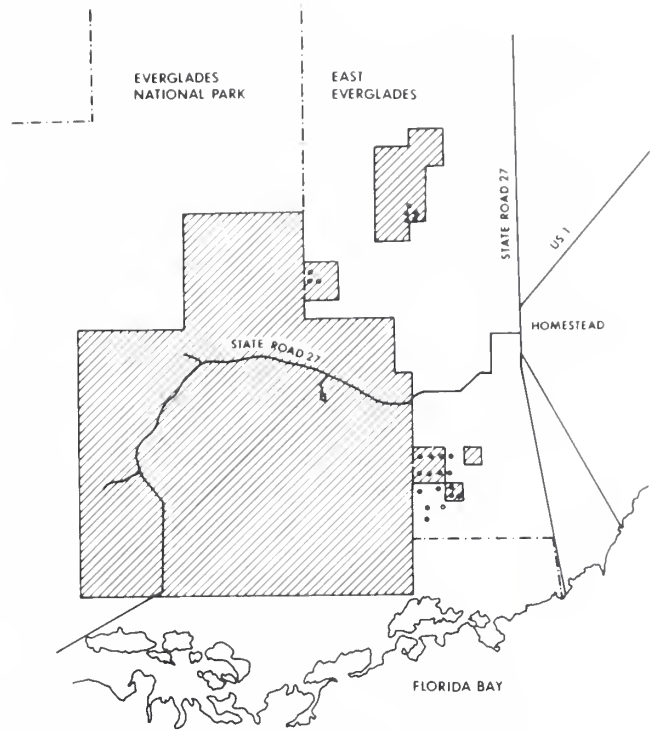


Fig. 8. Critical habitat of the Cape Sable Sparrow compared with current distribution of birds in the East Everglades. Much of the isolated habitat in the East Everglades is no longer suitable for the birds.

Nonetheless, as of 1981, a substantial population persists over a large area of freshwater Muhly and mixed-species marsh. The population is influenced by fire, water conditions, and plant community distribution. Peripheral population segments are threatened by man-caused habitat disruption, but the preponderance of the population is under Federal jurisdiction in Everglades National Park and Big Cypress National Preserve. We conclude that the status of the Cape Sable Sparrow is more secure than previously thought, but the persistence of marginal peripheral populations requires direct management, and the survival of the subspecies depends on maintenance of natural water and fire regimes.

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Fire Management and the Cape Sable Sparrow

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Abstract. The impact of fire on Cape Sable Sparrows was measured in *Muhlenbergia* prairies of Taylor Slough, Everglades National Park, Florida. The response of the sparrow population following fire depends on the rate of vegetation recovery, the soil depth, and the amount of exposed pinnacle rock. Sparrows reinvade shallow soil sites (less than 20cm deep) by about 4 years after fire, but populations may remain at only two to five males per 100 acres for up to 10 years. On deeper soils (over 40 cm), or on soils without pinnacle rock, birds are present the second breeding season after fire and increase in numbers through the fourth year. Other studies show populations probably decline after 4 years, as dead plant material accumulates. In the current study, birds apparently were forced to use a marginal site, unburned for about 10 years, because a large fire disturbed most other nearby habitat. Fires cause nesting sites to be clumped by forcing birds to use marginal areas following large fires, by creating long edges where birds concentrate, and by creating a mosaic pattern of unburned patches in which the birds nest.

The Cape Sable Sparrow (*Ammospiza maritima mirabilis*) is a subspecies of Seaside Sparrow confined to the extreme southern tip of Florida. The bird has been of interest since its discovery in 1918 for the following reasons: It was thought to have been the last species described in the continental United States; it was believed to have been extirpated by a hurricane, only to be rediscovered; and its limited distribution exposes it to various catastrophic threats such as hurricanes and fires. In addition, the Cape Sable Sparrow has been receiving attention because two other Seaside Sparrows, the Dusky and Smyrna, have recently disappeared from the wilds of Florida (Baker and Kale 1978a, 1978b; Kale, this symposium). According to Kushlan et al. (1982), the limited distribution and catastrophic history of the Cape Sable Sparrow resulted in its being classified as an endangered species under the original Federal listing of 1967.

Almost the entire habitat of the sparrow lies within lands administered by the National Park Service, in Everglades National Park and Big Cypress National Preserve. These two parks have the highest fire frequency of all national park lands, with combined annual fire totals often exceeding 50% of the total acreage burned on all National Park Service areas. Acreages

burned on these two parks during 1981 may exceed 80% of the total burned during the year on National Park Service lands.

Stimson (1956, 1968) felt fire was destructive to the Cape Sable Sparrow, and this was generally accepted until work by Werner (1975). Werner (1975) stated that the Cape Sable Sparrow appears to benefit from fire and that it may depend on fire for survival. He recommended that up to 20% of the sparrow habitat be burned each year.

This paper is a report on the impact of fire on the Cape Sable Sparrow in the Taylor Slough area of Everglades National Park (Fig. 1). The study was conducted from 1978 through 1981. Werner (1975) and Werner and Woolfenden (this symposium) have discussed in detail the biology of the bird in the same area (see Figure 1 for the location of Werner's plots). Kushlan and Bass (this symposium) discuss the distribution, habitat, and population status of the sparrow in southern Florida.

MATERIALS AND METHODS

Census Transects

Census transects were selected in deep and in shallow soils near Taylor Slough, Everglades National Park (Fig. 1). Table 1 shows the year each area was burned, year censused, years post-fire, and size of census area. Records show the entire area to have been fire free for

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about 10 years prior to a December 1977 prescribed fire. This fire burned 3,800 acres when the soil was dry, and all vegetation was removed. A June 1980 lightning caused fire burned a 1,200 acre mosaic pattern in portions of the 1977 burn area.

Transects were established in deep soils during the 1978 breeding season as follows (Fig. 1):

- Transect 1 was set on the 10-year-old unburned area.
- Transect 2 was set at the edge of the 10-year-old unburned area and the 1977 burn.
- Transect 3 was set on the 1977 burn area and was used to measure changes following the 1977 fire until it was burned again in June 1980. Thereafter, Transect 3 was used to follow changes resulting from the June 1980 lightning-caused fire.
- Transect 4 was established in 1981 in the 1977 burn area as a replacement for transect 3.

To measure impact of fires at varying frequencies and times of year, several study sites were selected on shallow soils on the west edge of Taylor Slough (Fig. 1). The area had been fire free for about 10 years. Each study site is approximately 50 acres in size and is scheduled to be burned during December, February, or July on an annual basis (D1, F1, J1 in Fig. 1); during December, February, or July on a 3-year rotation (D3, F3, J3 in Fig. 1), and on a 5-year rotation during December or February (D5 and F5 in Fig. 1). During the first year of the study, all plots to be burned at a specific season (i.e. D1, D3, D5) were burned at the same time resulting in burning a minimum of 150 acres on each of the seasonal plots. All burns resulted in complete removal of vegetation. Insufficient fuel was present at 1 year post-fire for fire to carry, and not until 2 years post-fire did the annual burn plots carry fire. The control site (C in Fig. 1) is to remain unburned.

Each census transect is in a *Muhlenbergia* prairie community type (Olmsted et al. 1980). Our measurements show *Muhlenbergia filipes* to have a frequency of 85 to 95% and coverage of 17 to 43%. Sawgrass (*Cladium jamaicense*) frequency ranged from 32 to 70% with coverage of 1 to 16%. The number of individual plant species ranged from 25 to 35 on the various sites. Soils, consisting of Perrine marl, were inundated by water approximately from 1 July through 1 November.

Bird Census

Breeding-bird censuses were conducted during April and May. Censuses were completed between 0500 and 0800, with notes made on cloud cover, wind speed, precipitation, and dewfall on vegetation. The transect method described by Emlen (1977) was used. Each of the 13 sites was censused a minimum of four times per season. Transect length varies from 500 yards (455 m) long to 1,200 yards long (1,092 m), depending upon size of the study site. Only on J1 and J3 sites were transect lengths less than 700 yards (637 m). All singing males within a 180-foot (55-m) strip were counted and included in census totals.

Plant Biomass Samples

Plant biomass was clipped at ground level from meter-square areas, placed in a plastic bag, and returned to the laboratory for sorting, drying, and

weighing. Samples were dried at 70-80°C, and weighed to the nearest gram. Periphyton was excluded from the sample. With the exception of the first sample period, 12 samples were collected by randomly tossing the sample frame three times from a corner of each of four permanent study plots within the treatment area.

Samples were separated into four categories: live Sawgrass, dead Sawgrass, live other (everything except Sawgrass), and dead other (everything except Sawgrass). Sample categories were combined to yield total biomass, total live biomass, and total dead biomass.

Soil Depths

Five soil-depth measurements were taken within each meter-square vegetation sample by measuring the distance from the soil surface to bedrock.

RESULTS

The Cape Sable Sparrow population remained fairly stable at between two and five males per 100 acres on the unburned control plot (Table 1, Fig. 2). Sparrows were present on D, F, and J plots before fires were set, but 2 years post-fire they had reappeared only on the J1 plot. Their presence on J1 may have been an artifact of the short distance to the surrounding unburned areas. For example, a number of birds were observed during each census along the unburned north edge of J1, J3, and D1 plots.

Sparrow populations on Transects 1, 2, 3, and 4 show a response to fire. It is unknown whether birds were present in the area before the December 1977 prescribed fire. Birds were not present on Transect 3 during the first breeding season following the fire (Fig. 2, Table 1), but sparrow numbers increased in each of the subsequent years. A lightning-caused fire burned Transect 3 in 1980, the third year after the December 1977 fire; so the census was moved to Transect 4, where the population was found to be comparable to that of Transect 3 the previous year (Table 1, Fig. 2). Population levels on Transect 3, the first breeding season following the June lightning-caused fire, were comparable to those on the unburned control plot.

Transect 2, along the edge between the December 1977 burn and the adjacent unburned prairie, had a relatively high population present the first year following fire (Table 1). All birds were along the edge in the unburned grass, in habitat similar to that of Transect 1, and none were found in the burned area. The second year post-fire, no birds were present on the transect, apparently because they moved onto the 2-year-old burn area.

Transect 1, unburned for approximately 10 years, had a population of sparrows only slightly higher than the unburned control plot (C in Fig. 1) the first breeding season following the December 1977 fire. Birds were not present on the site the second, third, and fourth years post-fire (Table 1, Fig. 2).

Cape Sable Sparrows occurred within certain limits of total plant biomass and dead plant biomass (Table 2). Birds occurred within a total biomass range of 350 to 700 gm/m². They occurred where dead plant biomass ranged from 250 to 550 gm/m². Extreme upper biomass limits occurred on Transect 1 where birds used the area only 1 year following the December 1977 fire (Table 2).

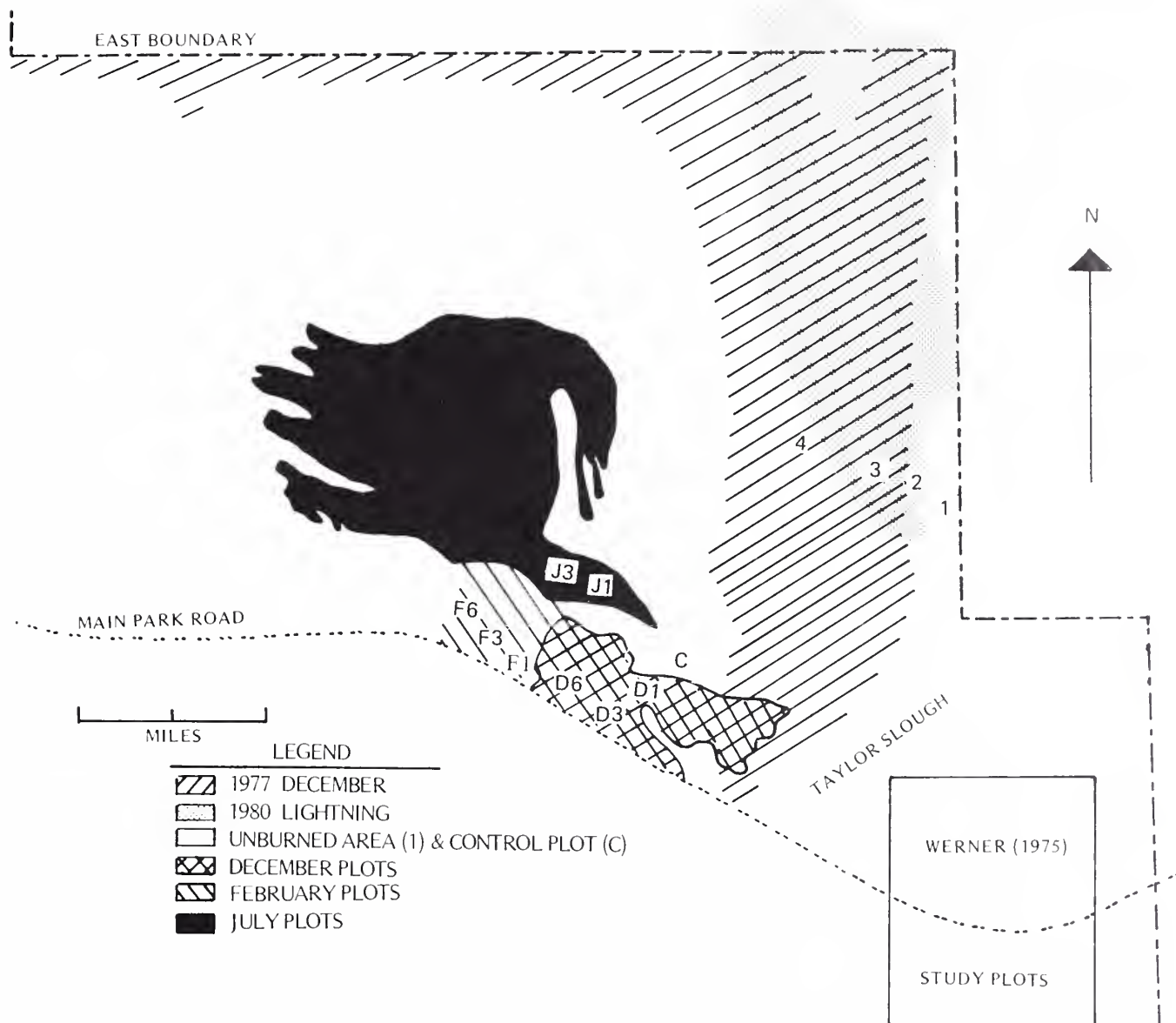


Fig. 1. Location of study plots near Taylor Slough, Everglades National Park, Florida. Transects followed a northerly route from the location of letters.

The second year post-fire, the transect did not appear changed physically, but birds had moved to the surrounding 2-year post-fire area. This result indicates that levels approaching 700 gm/m² for total biomass and 550 gm/m² for dead biomass are too high for continued use of an area by Cape Sable Sparrows.

Live/dead biomass ratios ranged from 0.28 to 2.94, depending upon the time following fire, but birds were present only on transects where ratios ranged from 0.28 to 0.61 (Fig. 3). The seven transects with ratios of 0.28 to 0.61 but without birds were on shallow-soil sites where lower total biomass occurred the first few years following fire. Thus birds had not yet recolonized such areas.

Soil depths ranged from 6.5 to 56 cm, and considerable variation occurred within each area (Table 2). Pinnacle rock was prevalent on the control plot and D through J plots. On these areas, soils were less than 20 cm deep, and total plant biomass ranged from 400 to

500 gm/m². Where soil depth exceeded 40 cm, as on Transects 1 through 4, maximum total biomass approached 700 gm/m² during the breeding season (Table 2). Cape Sable Sparrow populations recovered more rapidly following fire on prairies with deeper soils.

DISCUSSION

The patchy distribution of Seaside Sparrows has been referred to by several authors (Howell in Stimson 1968, Werner 1975, Post 1974). Post (1974) felt birds selected nest sites in areas where vegetation was relatively undisturbed by ice floes and winter tides, causing territories to be clumped. W. B. Robertson Jr. (Kushlan et al. 1982), in reanalyzing Werner's (1975) data, felt breeding density was most likely to be related to the complex fire mosaic within *Muhlenbergia* communities and the effects of fire severity and fire-free interval upon availability of nest sites. My data show fires can cause clumping of nest sites by three methods: (1) burn-

TABLE 1. Cape Sable Sparrow population estimates, in relation to time since fire.

Study Site	Date burned (month/year)	Census year	Years post-fire	Area censused (acres)	Number males per 100 acres
Control	about 1969	1979	10	14.9	3.4
		1980	11	14.9	1.7
		1981	12	14.9	5.0
D1	12-78	1979	1	9.3	0
		1980	2	8.7	0
		1-81	1	9.6	0
D3	12-78	1979	1	9.3	0
		1980	2	8.7	0
		1981	3	7.7	0
D5	12-78	1979	1	9.3	0
		1980	2	8.4	0
		1981	3	9.3	0
F1	3-79	1979	1	11.8	0
		1980	2	8.7	0
		3-81	1	8.1	0
F3	3-79	1979	1	11.8	0
		1980	2	8.7	0
		1981	3	8.4	0
F5	3-79	1979	1	11.8	0
		1980	2	8.7	0
		1981	3	9.0	0
J1	7-79	1980	1	8.1	0
		1981	2	6.5	7.7
J3	7-79	1980	1	8.4	0
		1981	2	8.1	0
Transect 1	about 1968	1978	10	14.9	6.7
		1979	11	14.9	0
		1980	12	14.9	0
		1981	13	13.0	0
Transect 2	edge-12-77 edge-about 1968	1978	1/10	14.9	13.4
Transect 3	12-77	1978	1	14.9	0
		1979	2	14.9	11.7
		1980	3	14.9	30.2
		6-80	1	13.0	3.9
Transect 4	12-77	1981	4	14.9	35.2

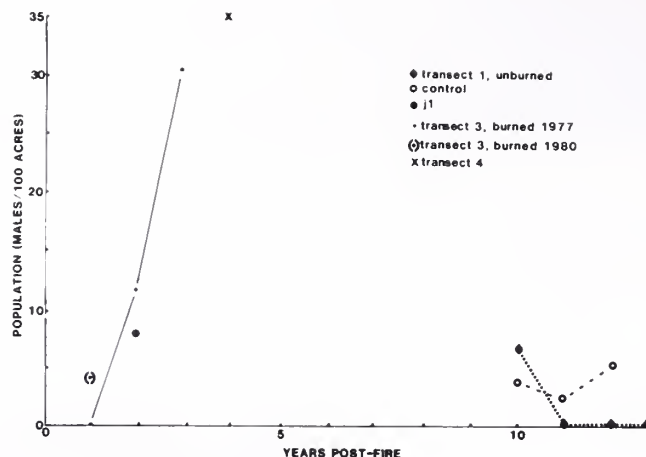


Fig. 2. Breeding-season population estimates of Cape Sable Sparrows.

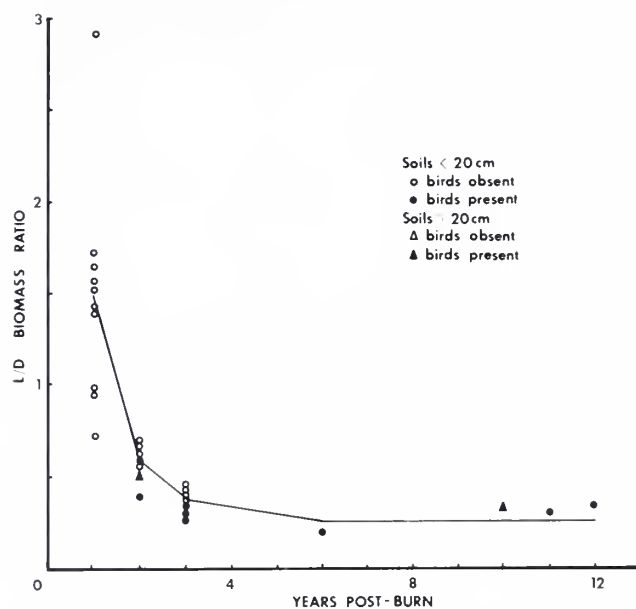


Fig. 3. Ratio of live to dead plant biomass following fire.

ing large acreages and forcing birds to nest in unsuitable habitat; (2) creating an edge along a larger burn where birds concentrate during the first breeding season following fire, and perhaps in subsequent years; and (3) creating a mosaic pattern of burned and unburned patches, with unburned patches used for nest sites during the first and possibly later breeding seasons following fire. Examples follow.

Cape Sable Sparrows were present on Transect 1, unburned for about 10 years, the first breeding season following the contiguous December 1977 fire, but birds were no longer present during the second, third, and fourth seasons post-fire (Table 1). At the same time, birds were absent from burned Transect 3 the first year post-fire, but they were present in increasing numbers the second, third, and fourth years (Table 1). A survey of the 3,800-acre burn area showed birds to be present only in the vicinity of Transect 3 the second year post-

fire, but the third and fourth years, birds were distributed throughout the burn site. These results suggest the 3,800-acre December burn disturbed such a large amount of available habitat that the Cape Sable Sparrow was forced to use a marginal area on Transect 1 for 1 year. Plant biomass measurements from Transect 1 were consistently at the extreme upper limits for areas where sparrows occurred. Sparrows moved into only the edge of the December burn the second year post-fire, but by the third year, they had occupied the 3,800 acres.

Concentration of birds along edges of burns is illustrated by data from Transect 2, which was established on the boundary of the December 1977 burned area and the unburned grass of Transect 1. One of the higher populations of sparrows was measured on this transect the first year following fire (Table 1), but the birds were concentrated in the unburned grass and none

TABLE 2. Relationship of plant biomass (gm/m²) during the breeding season to years post-fire and soil depth.

Study site	Years post-fire	Plant Biomass							Soil depth (cm)
		Total	Dead	Live	Live other	Dead other	Live Sawgrass	Dead Sawgrass	
Control	11	394±176	310	84	51±24	221±143	33±22	89±78	15.3± 6
	12	341±109	265± 82	76±31	44±12	160± 48	32±23	105±57	
D1	1	63± 19	16± 9	47±15	42±15	12± 5	5± 5	4± 6	12.4± 4
	2	147± 45	89± 24	58±22	44±21	74± 23	14±12	15±10	
	1	43± 10	25± 7	18± 5	14± 4	17± 6	4± 2	8± 6	
D3	1	71± 16	26± 14	45±20	34±15	25± 14	12± 9	1± 1	12.0± 4
	2	133± 41	81± 27	52±15	38±17	59± 29	14± 9	21±17	
	3	315± 75	219±52	96±28	79±21	175± 33	16±10	44±26	
D5	1	52± 21	18± 8	30±15	18±11	13± 5	11± 8	5± 5	6.5±5
	2	101± 27	59± 19	41±13	26±10	40± 12	15± 8	20± 9	
	3	154± 49	110± 39	44±14	27± 9	60± 38	17± 8	49±23	
J1	1	128± 41	65± 24	63±21	50±17	54± 25	13± 9	11± 9	18.2± 7
	2	181± 26	113	69	57±14	93± 16	12± 6	20±11	
J3	1	85± 20	44± 14	41± 9	34± 8	38± 15	7± 4	6± 3	15.0± 6
	2	165± 39	104± 26	61±16	46±12	79± 21	15± 8	25±16	
F1	1	65± 23	25± 9	39±19	27±16	21± 7	12± 9	4± 5	16.2± 8
	2	153± 36	96± 28	57±10	37± 9	75± 24	20± 9	21±10	
	1	57± 17	23± 10	35±14	28±14	12± 6	7	11± 7	
F3	1	100± 20	52± 23	74±39	50±26	44± 21	18±16	5± 6	18.3± 7
	2	145± 37	86± 21	59±17	44±18	71± 24	15±11	15± 9	
	3	283± 95	200± 67	83±30	59±21	145± 48	24±12	55±37	
F5	1	74± 27	31± 14	44±19	38±16	29± 14	6± 8	2± 3	18.1± 8
	2	164± 46	104± 28	60±19	43±20	78± 30	17±10	25±19	
	3	273±114	190± 83	84±33	69±26	160± 94	14±12	30±25	
Transect 1	10	698	550±165	148±37	125±43	516±169	23±20	35±36	56.0± 9
Transect 3	2	387	257± 43	130±46	108±47	228± 43	22± 9	29±11	42.0±21

were present on the burned area. The second year post-fire, no birds were observed on the transect as they apparently had moved from the unburned grass to the 2-year-old burn area. Presence of sparrows along burned edges was also noted after plots D1, J1, and J3 were burned (Fig. 1).

After Transect 3 was again burned during June, and a mosaic pattern resulted from the fire, 3.9 males per 100 acres were present, and all bird activity was within or around unburned patches. On no other transect were birds found nesting during the first breeding season following fire.

Time of year when fires occur is an important influence on the mosaic pattern. Dry-season fires (November to June, depending upon the year) burn all vegetation, including small hammocks. Wet-season fires (June to November) have more potential for burning in a mosaic pattern, but in all seasons, water level is the determining factor. For example, when the December 1977 fire burned all vegetation including small hammocks, water level at the Taylor Slough Bridge was 2.57 feet mean sea level (msl). Water level of 3.02 feet msl during the July prescribed fire on the J plots resulted in few hammocks being burned, but there was no burned-unburned mosaic left in the grass. A mosaic pattern resulted from the June 1980 lightning fire, which burned when the water level was 3.89 feet msl.

Cape Sable Sparrow populations ranged from 0 to 35.2 males per 100 acres, depending on the time following fire (Table 1, Fig. 2). Sparrows were absent the first year following fire on transects with soils over 40 cm deep, but the population increased the second, third, and fourth breeding seasons (Fig. 2). What will happen after 4 years is unknown from this study, but the population is expected to decline. Werner (1975) found Cape Sable Sparrows began to use *Muhlenbergia* prairie approximately 1 year after a fire and that density increased through the third year post-fire. After the fourth year, he felt that density would decline. Werner (1976) reported the following populations following fire in Taylor Slough (numbers/100 acres): year 1, 0; year 2, 11 and 13; year 3, 20; year 4, 4; year 5, 4; year 6, 0. He showed maximum plant biomass was attained within 3 years after burning, and that the ratio of live to dead biomass was lowest after 3 years. He concluded that dead biomass accumulates and causes the habitat to become unsuitable for sparrows.

My data from Transects 3 and 4 support Werner's conclusions, but results from other transects show Cape Sable Sparrow response depends on soil depth and soil volume above bedrock and on vegetation recovery. On areas where soil depth is 40 cm or greater, vegetation recovery is rapid, and sparrow populations recover, reach maximum levels, and possibly begin to decline

TABLE 3. Percent of plant biomass recovery to pre-fire biomass level. See Table 2 for soil depth at each study site.

Study site	Year 1	Year 2	Year 3
J1	45	64	—
J3	23	46	—
Mean	33	54	—
F1	16	39	—
	14	—	—
F3	16	23	45
F5	16	37	62
Mean	16	35	64
D1	29	68	—
	20	—	—
D3	17	33	78
D5	16	32	49
Mean	18	41	76
Transect 3 (December burn)		55	

after 4 years post-fire. By 2 years post-fire, total plant biomass approaches or exceeds biomass from the control plot (10 years post-fire) where soils are less than 20 cm deep (Table 1). Sparrow population recovery on the D through J plots, where soils are 20 cm or less in depth, and where considerable pinnacle rock occurs, was only beginning by 4 years post-fire. Apparently, by 4 years, plant biomass levels have not recovered to the point where birds normally occur (Table 2). Werner's (1976) population estimates more nearly follow results from areas with soils 40 cm deep even though he measured soil depths of 14 to 20 cm. The difference in our results is because total soil volume above bedrock was greater on his study areas, a fact easily observed by the lack of pinnacle rock there.

Plant biomass recovery takes at least 4 years on shallow soils having a low volume per unit area, compared to about 3 years on sites with deeper soils (Werner 1975). (See Table 2 for soil depth at each study site.) Apparently, sparrow populations are always relatively low (2 to 5 birds/100 acres) on sites with shallow soils. Because much of the Cape Sable Sparrow habitat is on *Muhlenbergia* prairies with shallow soils, fires that burn more frequently than every 8 to 10 years will be detrimental to the population.

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Breeding Seaside Sparrows in Captivity

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Abstract. Two years' experience with eight pairs of captive Seaside Sparrows (*Ammospiza maritima*) shows that Dusky (*A. m. nigrescens*), Scott's (*A. m. peninsulae*), and Dusky × Scott's Seaside Sparrows will breed in captivity. The overall reproductive success of these captive breeders was about equal to that of wild Seasides. Our captives bred successfully whether 1, 2, or more years old; whether experienced or inexperienced at breeding; whether mated to a bird of the same or another subspecies; whether wild-caught, hand-raised, or raised in captivity by their parents; and whether outcrossed or inbred.

Only five Dusky Seaside Sparrows are known to exist; all are in captivity and all are males. In order to make up for the lack of Dusky females, we suggest that the male Dusks be mated to female Scott's Seaside Sparrows, that F_1 females be backcrossed to the Dusks, and that such backcrosses be continued for several generations. The F_1 progeny of our one Dusky × Scott's mating are fertile. Our F_1 and F_2 Dusky × Scott's intergrades and our backcrosses to Scott's resemble Dusks in proportion to their degree of Dusky ancestry. The results of these matings strongly suggest that a few generations of backcrossing to the Dusks would suffice to produce offspring indistinguishable from the original Dusks.¹

Five subspecies of Seaside Sparrows (*Ammospiza maritima*) are endemic to Florida, and the breeding range of another lies partly within the state. Each of these five endemics, and the one regional population, is either near extinction, declining in numbers, or considered to be in danger of decline (Kale 1978).

The one Florida race of the Seaside Sparrow that is most clearly endangered in its entirety is *A. m. nigrescens*, the Dusky Seaside Sparrow. The Dusky, and *A. m. mirabilis*, the Cape Sable Seaside Sparrow, are the only races of the Seaside Sparrow listed as "endangered" by the U.S. Fish and Wildlife Service (Kale 1978). Both of these subspecies are geographically isolated, and each represents the southernmost extension of the Seaside Sparrow on its respective coast. Each has evolved distinctive plumage coloration and songs. Several thousand Cape Sables remain, but the Dusky is probably extinct in the wild.

The Dusky's decline has been especially rapid. In 1968 there were about 900 males, and, it is presumed,

an equal number of females (Sharp 1970). By 1981 only five known Dusks remained. All are males. These five birds now live in custom-built aviaries at the Santa Fe Community College Teaching Zoo in Gainesville, Florida. No Dusks have been seen in the wild since 1980.

In response to the Dusky's decline, the Florida Game and Freshwater Fish Commission began a recovery program in 1979. This program had three objectives.

The first objective was to find and capture more wild Dusks. Females were especially wanted, of course. The search continues, but no more Dusks have been found as of midsummer 1981.

The second objective was to study the behavior and ecology of one of the Florida races of the Seaside Sparrow closely related to the Dusky. Although the biology of the Northern Seaside Sparrow (*A. m. maritima*) is fairly well known (Woolfenden 1956, Post 1974, Post and Greenlaw 1975), little was known about the behavior of the southern races. Because so little was known about the Dusky Seaside Sparrow's reproductive biology, other than Trost's (1968) pioneering study, and because the bird had become extremely rare by 1975 (Baker 1978), it was necessary to study another population of Seaside Sparrows in order to get basic information on such subjects as reproductive success, predation, habitat selection, food, and adult survival. The subspecies chosen for this aspect of the study was *A. m. peninsulae*, Scott's Seaside Sparrow, of the peninsular Gulf

¹Many of the 1980 data in this paper are published in a shortened and modified form in Post and Antonio (1981). The present paper is a review of all captive breeding of Seaside Sparrows, including presentation of new results. Even though the present authors did different parts of the work described here, we use the pronoun "we" nearly throughout in order to avoid circumlocutions. Most of the work in 1980 was done by Post. The 1981 work was done by Webber and Post.

Coast of Florida. Of the various populations of the Seaside Sparrow, the Gulf Coast groups are the most similar to the Dusky ecologically and morphologically. In January 1979 Post established a field study site at Cedar Key, Levy County, at about the same latitude as Gainesville. The study population consisted of 345 color-banded individuals. During a 2-year period he studied 146 nestings of this population.

The third objective was to devise means of breeding Seaside Sparrows in captivity, and ways of releasing these captive-bred birds into the wild so that they would stay where they were put. We hoped, of course, to begin a captive breeding program with both male and female Dusks. Implicit from the beginning, however, in view of the possibility that no females could be found, was the necessity of testing the last-ditch alternative, namely, an initial mating of the Dusks with females of a closely related subspecies, such as Scott's Seaside Sparrow. By this approach, the male Dusks would first be mated to female Scott's, and the resulting female offspring would be backcrossed to the Dusks in the following year. The female offspring of these backcrosses would themselves be mated to the Dusks, and so on for the desired number of generations. The female Scott's would be used only in the parental generation to make up for the lack of any female Dusks. Because the principal known differences between the Dusky and other Seaside Sparrows are the Dusky's dark color and heavy streaking on the underparts, the practical approach would be to breed selectively the offspring in each generation that look most like Dusks.

In 1980 the captive breeding program began as planned. Several pairs of Scott's Seaside Sparrows bred in our aviaries with gratifying success. We learned something about the species' requirements for captive breeding, and made the first steps in the backcrossing scheme by raising a brood of Dusky \times Scott's intergrades.

In early 1981 the entire character of the Dusky recovery program changed when the Game Commission gave up control of the Dusks, and the U.S. Fish and Wildlife Service gave \$46,000 to Santa Fe Community College to house and care for them. The USFWS now has legal control of all five Dusks and as of this writing will not allow them to be used in any sort of breeding program. When the Dusks changed hands, we transferred one of the Scott's Seaside Sparrows and the three F_1 Scott's \times Dusky intergrades to our aviaries at the University of Florida. Because we had no money, our breeding program in 1981 was informal and makeshift. Our aviaries were made of scavenged materials, the work was done in our spare time, and we simplified food, feeding, and observations. Without the Dusks, we could not form the breeding pairs that we most wanted, but we tried to use the birds that we had to answer some of the most important questions remaining about the usefulness of captive breeding in saving the Dusky. We especially wanted to find out whether the F_1 Dusky \times Scott's intergrades were fertile, and whether the F_2 intergrades and backcrosses to Scott's would look at all like Dusks.

Unless we say otherwise, the statements that follow refer to all of the sparrows, in 1980 and 1981. Because the circumstances in 1981 were so different from those in 1980, the data for these 2 years are often given

separately. In order to make better chronological sense, some information is given out of place; for instance, some results are described under Materials and Methods.

MATERIALS AND METHODS

Origins of Captives

Six nestling (ages 4 to 6 days) *A. m. peninsulae* were taken from the Cedar Key study area in April 1979 for hand-rearing. Eighteen free-flying adult and juvenile *peninsulae* were captured in August 1979. One additional juvenile (second year) female was taken in February 1980. We captured three adult male Dusks in August and September 1979. All of our breeders were from among these birds, or their offspring born in 1980.

Pairs Formed in 1980

We distributed some of these Seaside Sparrows, by pairs, among our aviaries in February 1980. These consisted of one *peninsulae* \times *nigrescens* pair and five *peninsulae* \times *peninsulae* pairs. Some breeders were hand-raised (HR), others wild-caught; some were yearlings (SY), others 2 years old or older (ASY). See Table 1 for pairs, aviaries, and locations.

Pairs Formed in 1981

In early 1981 the Dusks went to Santa Fe. Out of all of the remaining Seaside Sparrows, wild-caught or captive-raised, we retained only four at our aviaries at the University of Florida, and released the rest. Three of these four were the offspring of the *nigrescens* \times *peninsulae* pair, a male and two females, all brood-mates. The fourth was a male Scott's Seaside Sparrow taken from the nest at Cedar Key in 1979 and hand-raised. On 27 February we placed one of the intergrade females with the male *peninsulae* in one aviary, and in the adjacent aviary placed together the other female intergrade and her brother (Fig. 1).

Housing

In 1980, five of our breeding aviaries (four Scott's pairs, one Dusky + Scott's pair) were grouped together in a compound at the Game Commission research lab in Gainesville, and one (a Scott's pair) was at the Teaching Zoo, several miles away. Because territories are clumped in some wild populations (Post 1974), we wanted to know whether the birds would nest in solitary pairs, or whether they needed the stimulation of seeing and hearing other Seaside Sparrows. In 1981 our two aviaries, at the University of Florida, were side-by-side, and separated only by a transparent partition.

We tested aviaries of five shapes and eight sizes. One of these was formed from four interconnecting hexagons, each 3 m on a side and 3 m high. This aviary had a galvanized angle-iron frame, and was covered with 1/4-inch-mesh hardware cloth. Two others were equilateral triangles, 4.7 m and 3.7 m on a side, 1.8 m high. One aviary was a rectangle 7 m by 2.5 m, and another was 3.7 m square. The last four aviaries had frames of heavy cypress beams, covered with a fine-mesh (about 1 \times 3 mm) plastic cloth.

The foregoing five aviaries, at the Game Commission, were surrounded by a 3-m-high wooden fence, which was encircled at 0.5 m and 3 m by electric shock

TABLE 1. Reproductive performance of captive pairs of Seaside Sparrows compared to that of a wild population.

1980

Aviary ¹	Male	Female	Cycle no.	Date clutch completed	No. eggs	No. young	No. fledglings	Possible/probable causes of mortality
B	ASY ² <i>peninsulae</i>	SY <i>peninsulae</i>	1	11 May	1	0	0	desertion
C	ASY <i>nigrescens</i>	SY <i>peninsulae</i>	1	14 May	3	3	3	
D	ASY <i>peninsulae</i>	ASY <i>peninsulae</i>	1	3 May	3	2	1	1 egg: doesn't hatch 1 young: starvation
			2	6 June	4	0	0	4 eggs: unknown predator
E	ASY <i>peninsulae</i>	SY <i>peninsulae</i>	-	-	-	-	-	did not nest
F	HR <i>peninsulae</i> 1Y	SY <i>peninsulae</i>	1	1 May	4	3	2	1 egg: doesn't hatch 1 young: starvation
			2	29 May	3	1	1	2 young: starvation
			3	30 June	3	2	0	1 egg: doesn't hatch 2 young: starvation
			4	18 July	3	2	1	1 egg: breaks during incubation 1 young: starvation
SF	ASY <i>peninsulae</i>	HR <i>peninsulae</i> 1Y	1	10 April	3	3	2	1 young: starvation
			2	9 May	3	2	2	1 egg: doesn't hatch
			3	8 June	3	2	0	1 egg: doesn't hatch 2 young: starvation
			4	29 June	3	0	0	3 eggs: unknown
Total, Captive Population, 1980			12 nestings		36	20	12 (33%) ³	
Total, Control ⁴ Population, 1980			8 nestings		25	15	9 (36%)	

1981

Aviary	Male	Female	Cycle no.	Approximate date clutch completed	No. eggs	No. nestlings	No. fledglings	Possible/probable causes of mortality
G	2Y, HR <i>peninsulae</i>	1Y, CB <i>nigrescens</i> × <i>peninsulae</i>	1	17 April	3	2	2	harassment?
			2	18 May	4	4	3	
			3	2nd week June	≥2	0	0	predation
H	1Y, CB <i>nigrescens</i> × <i>peninsulae</i>	1Y, CB <i>nigrescens</i> × <i>peninsulae</i>	1	26 April	2	2	2	harassment?
			2	25 May	4	4	4 ⁵	
			3	3rd week June	≥3	0	0	predation
Total, Captive Population, 1981					≥18	12	11 (≤61%)	

¹ Aviary B was a 3.7-m square, grouped with aviaries C-F; C: four interconnected hexagons, each 3 m to a side; D: a 7 × 2.5-m rectangle; E: a 3.7-m equilateral triangle; F: a 4.7-m equilateral triangle; SF: two interconnected decagons, each 4-m diameter, the only isolated aviary; G: a rectangle 2.4 m × 6 m; H: a rectangle 2.4 × 7.6 m.

² Age and treatment designations: ASY = caught as an adult the previous year, exact age unknown; SY = caught as a juvenile the previous year; HR = hand-reared; CB = captive-bred; 1Y = yearling; 2Y = years old.

³ Percentage of eggs that produced fledglings.

⁴ Control population consisted of eight nests of wild pairs, each protected by a metal predator baffle.

⁵ One of these four died by choking after reaching fledging age, so that Figure 1 shows only three birds in this brood.

wire. The hexagonal aviary, in which the Duskie were held, was surrounded by a galvanized sheet-metal predator baffle, embedded 0.3 m into the ground, and extending 1 m above the ground.

The Teaching Zoo Aviary consisted of two interconnected decagons, each with a diameter of 4 m.

In 1981 our two aviaries, at the University of Florida, were both 2.4 m wide and 2 m high. One was 7.6 m long, the other 6 m. The frames were constructed of cedar slats, covered with fine-mesh plastic cloth. They abutted to form an L. They were entirely surrounded by a predator baffle of heavy nylon cloth that extended 1 m

below and above the ground.

We planted all aviaries with clumps of Cordgrass (*Spartina bakeri*), placed 0.5 to 2 m apart. Cordgrass was used because wild Dusks nest in it (Trost 1968) and because it requires only periodic inundation. In 1980, but not 1981, we also planted small patches of other grasses, mainly *Fimbristylis* and Guinea Grass (*Panicum maximum*) amid the Cordgrass, and sprinkled the enclosure with rock salt to inhibit the growth of soil micro-organisms and weeds. Each aviary was provided with a pond or small stream of water.

Hand-raised nestlings were kept in cardboard boxes with a heating pad for the first few days. Once they could stand up they were put in cages about 1 m on a side; we removed the heating pad on day 12 (hatching day is considered day 0). In 1981 we put our two hand-raised broods together in an indoor cage about 2m × 2m × 2m, when they were 2 months old. We noticed no aggression when the two broods were mixed in this way.

Feeding

Adult Seaside Sparrows are easy to feed. Flying captives, both hand-reared and wild-caught, preferred canary seeds, but also ate thistle, and red and white millet. We provided the seeds both dry and soaked. In 1980 we provided crickets *ad libitum*. The sparrows' preferred live food was mealworms, but usually we provided no more than three larvae per bird per day.

Like other emberizines, Seaside Sparrows feed their young primarily animal food. During the summer of 1979 we ascertained the diet of wild nestlings at Cedar Key by the esophageal ligature method (Orians 1966). The main foods brought to the nestlings were grasshoppers and spiders, with hemipterans, homopterans, diptera, and small fiddler crabs *Uca* making up most of the rest of the diet (see Post et al., this symposium).

We found that captive parents feeding nestlings less than 3 days old forage selectively for insects less than 10 mm long. Provision of soft-bodied arthropods of this size may be crucial for the survival of young less than 3 days old.

At the start of the 1980 breeding season (late March), we began to provide wild-caught insects, mainly grasshoppers, that we caught by sweeping vegetation. We also caught beetles, moths, and leaf-hoppers in an ultraviolet light trap. Captives ate all of these items, preferring hemipterans and homopterans.

When adults were feeding young in 1980, we also provided the seeds named earlier, the diet devised by Lanyon and Lanyon (1969), and several commercial insectivorous bird mixes (Sluis Bekfin, Petamine). We added wheat germ oil and vitamins (Vionate or Avitron) to the wet seeds and Bekfin/Petamine.

Five of the six nestlings taken from the wild in 1979 were successfully hand-raised on the Lanyon diet, supplemented by wild-caught insects, mainly flies.

In 1981 we simplified the birds' diet. Nonbreeding adults received nothing but millet sprays, canary seeds, and dry Bekfin/Petamine (with no vitamins added). When the adults were feeding young, we changed this diet merely by adding water and vitamins to the Bekfin/Petamine (though as it turned out they fed little or none of this to the young), and by providing crickets and a few mealworms.

In 1981 we raised two broods of young by hand from day 6 to independence. The basic food they received when dependent upon hand-feeding was Purina High Protein Dog Chow, which we soaked in water and mashed to a smooth puree. To this we added vitamins and wheat germ oil, and fed it to the young with a hypodermic syringe. While they were of nestling age, we also fed them some moistened, vitamin-fortified Bekfin with forceps, but gave them no Petamine because it has so many large, sharp seeds in it. Once the young were about 20 days old we mixed the Bekfin with Petamine about half-and-half. Crickets and wild-caught insects constituted less than 20% of their diet.

Our hand-raised young, all taken from the nest on day 6 or earlier, begged readily for food and were easy to feed, except for the "50-percenters" (see Fig. 1) of 1981. We describe their idiosyncracies to forewarn future Seaside Sparrow aviculturists.

Of the three surviving birds of this brood, one had to be coaxed to open its mouth by bobbing the forceps or syringe up and down in front of its beak. It would follow the movement of the food with its head for as many as 30 to 40 repetitions until it finally opened its mouth briefly at the top of the upward movement, during which time the feeder had to maneuver the food into its mouth, or begin all over again. Another bird in the same brood would open its mouth readily enough to give begging sounds, but while it did so it would continually back away from the food. It had to be herded into a corner where it usually continued its evasive tactics with its head alone, all the time begging with wide-open mouth. Trying to get the food in was like trying to push together the similar poles of two powerful magnets. The third bird gave us none of these problems.

A few times one of these hard-to-feed young persisted in evading its food for so long that we resorted to force-feeding. When we force-fed, we used insects that would stay in one piece, so that nothing liquid or crumbly could make its way down the trachea. Even so, one of the original four 50-percenters raised by hand apparently choked to death on a fragment of food after force-feeding. Our impression was that the 50-percenters were a bit more precocious in their behavior than the 25-percenters. Therefore, at day 6 they may have been slightly too old to change over smoothly to being fed by people.

We fed the hand-raised young all they would eat every half-hour until about day 15, after which we fed them every 45 minutes to 1 hour. Beginning about day 15, we provided millet and canary seeds in a dish, and from then until they were independent of hand-feeding we gradually reduced the amount of dogfood in the diet to zero (thus increasing the proportion of Bekfin/Petamine). We stopped hand-feeding the young of both broods on the same day (4th of July), when the 50-percenters were 28 days old, and the 25-percenters were 35 days old. By the time they were able to feed themselves completely, they ate some millet but little canary seed, and the Bekfin/Petamine was still moistened with vitamins added. We continued giving them this diet for about 3 weeks after they were independent of hand-feeding, until, as an experiment, we abruptly substituted the dry Bekfin/Petamine; they devoured it

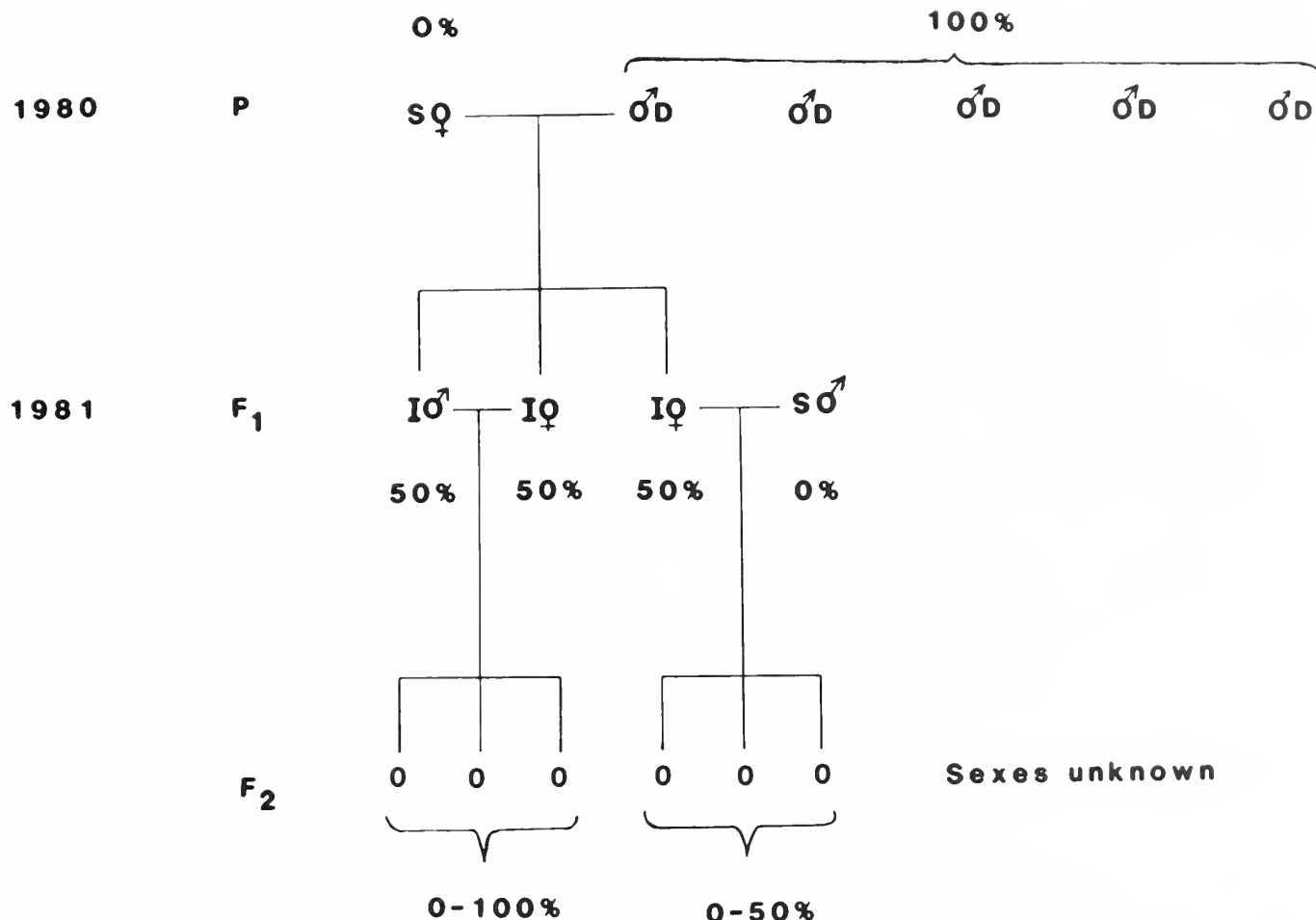


Fig. 1. Crosses performed between Scott's, Dusky, and intergrade Seaside Sparrows. We refer to the offspring of the Dusky \times Scott's pair, and of the brother-sister pair, as "50-percenters"; we call the offspring of the Scott's-intergrade pair "25-percenters". Technically speaking, the offspring of the Scott's-intergrade pair should be referred to as back-cross progeny, not F_2 's. The young shown in each brood are those that survived to the age at which they were independent of hand- or parental-feeding. D = Dusky, S = Scott's, I = intergrade.

without hesitation. At this point they were eating the normal adult diet.

Nests in the Wild

In 1980 Post surrounded eight nests of Scott's Seaside Sparrow at Cedar Key with sheet-metal baffles to exclude ground predators. We used the results of protected and unprotected nestings to evaluate the success of captive breeding.

RESULTS

In general, the behavior of the captives differed in no qualitative way from that of wild birds. They gave all of the postural displays and vocalizations described for the species by Post and Greenlaw (1975).

Timing of the Breeding Season

In 1980, regular singing by captives began in early March, at which time males also began giving flight songs, usually while clinging to the tops of their aviaries. On 5 April we found the first cloacal protuberance (6 mm), on an adult caught the previous August. When captive females became sexually receptive, in early April, they often gave whinny vocalizations (Post and

Greenlaw 1975). At this time females began to supplant males, and female dominance remained evident throughout the breeding season. The timing of these events corresponded to those at Cedar Key.

In 1980 the first nest building by a female was seen on 29 March. This female, of the isolated pair, laid her first egg on 8 April. At Cedar Key the first egg of 1980 was laid on 23 March. The last nest in the captive population was still active on 8 August, whereas the corresponding date for the Cedar Key population was 27 June. Thus, in 1980 the captives continued to breed for nearly a month longer than did wild birds.

In 1981 we first noticed singing on 27 March. The female of Pair G (pairs have the same letters as their aviaries; see Table 1) laid its first egg about 18 April, the female of Pair H on 24 April. The 1981 breeding season ended on 23 June, when predators, probably rodents, destroyed both pairs' third nests, and killed three of the four breeders (Table 1).

Recycling Time and Nest Loss

Pairs that lost all of their eggs or nestlings began a new nesting cycle sooner than did those that spent at least some time caring for fledglings. In 1980, the mean

time from completion of a clutch that produced fledglings until the completion of the subsequent clutch was 31 days ($N = 5$). The comparable time for clutches that did not produce fledglings was 19.5 days ($N = 2$). A possible source of bias is that the successful nestings tended to be earlier in the season, when breeding activities may have been slower anyway.

Nests and Nest Building

The captives obtained nest material from the marsh plants growing in their aviaries. In 1980 we provided supplementary material (dried grass), but did not do so in 1981.

Males occasionally carried nest material and placed it in grass clumps. We do not know whether females used any of these sites for nest placement. The breeding male Dusky made grass deposits that could have made adequate nest bases, but the female Scott's to which he was mated never used any of them.

Nests were placed 0.1 to 0.7 m above the ground. In 1980, six were in *S. bakeri*, four in *P. maximum*, and two in *Fimbristylis*. In 1981, all six nests were in *S. bakeri*, the only marsh plant in the aviaries in that year. In all cases of renesting in 1980 (one by one female, and three each by two others), the females placed the new nest in the same clump as the first. In 1981, Pair G (Scott's \times intergrade) built their first and second nests in different clumps, 1.5 m apart, and the third in the same clump as the first. Pair H (brother-sister pair) built their first and second nests in different clumps 0.6 m apart, and their third in the same clump as the second. The reuse of nest sites is not known in wild Seaside Sparrows. Such behavior by captives is probably the result of the scarcity of nest sites.

Incubation and Brooding

As is normal for wild Seaside Sparrows, only the females incubated and brooded, and both sexes delivered food to nestlings and fledglings. The initiation of male feeding varied between pairs. In 1980 one male *peninsulæ* began feeding nestlings the day after hatching, whereas the male *nigrescens* did not feed his young until the fourth day.

Hatching Success

In 1980 five pairs produced a total of 36 eggs (the sixth pair did not nest) in 12 nesting attempts, for a mean clutch size of 3. These 36 eggs produced a total of 20 nestlings (56%), for a mean of 1.7 nestlings per clutch.

The same year, eight pairs in the wild produced a total of 25 eggs in eight nesting attempts that were protected from ground predators, for a mean clutch size of 3.1. These 25 eggs produced a total of 15 nestlings (60%) for a mean of 1.9 nestlings per clutch.

In 1981 our two captive pairs produced a total of at least 18 eggs in six nesting attempts, for a mean clutch size of at least 3.0. These 18 eggs produced a total of 12 nestlings (67%), for a mean of 2.0 nestlings per clutch. If we count only the four nests not damaged by predators, then at least 13 eggs were produced by two pairs in four nesting attempts, for a mean clutch size of at least 3.25. These 13 eggs produced a total of 12 nestlings (92%), for a mean of 3 nestlings per clutch (Table 1).

The large second clutches laid by both females in 1981 (Table 1) may be the result of the abundance of

crickets provided them between the first and second nestings. In 1981, crickets and other live food were not given before the first and third nestings.

Fledging Success

In 1980, 12 of the 20 nestlings fledged (60%), for a mean of 1.0 fledgling per clutch. Thus, total egg success was 12/36 (33%). These 12 fledglings consisted of 9 *peninsulæ* and 3 *F. nigrescens* \times *peninsulæ* intergrades.

In the eight comparison nestings in the wild, 9 of the 15 nestlings fledged (60%), for a mean of 1.1 nestlings per clutch. Thus total egg success was 9/25 (36%) (Table 1).

In 1981, each of our two pairs fledged two young from its first nest. For reasons unknown all four of these young were dead within a month. Pair G then produced a second brood of three nestlings, and Pair H a second brood of four. We raised the second broods of Pairs G and H by hand. All were raised past fledging age, but one of the four Pair H "fledglings" died by choking. The third nests of both pairs were destroyed by predators before the nestling stage. Thus, out of 12 nestlings, 11 can be considered to have fledged (92%). If all six nestings are considered, egg success was 11/ \geq 18 (\leq 61%). If the two destroyed nests are discounted, egg success was 11/13 (85%) (Table 1).

Age at Independence from Parents

In 1980 we usually separated the aviary-bred fledglings from their parents at about the time that the eggs of the next clutch hatched. We removed four fledglings from their parents' aviary on day 29, two on day 31, and one on day 25. All of these young survived long past the time at which their deaths could be attributed to premature separation from their parents.

Appearance of Intergrades and Backcrosses

The objective of recovery-by-backcrossing is to make up for a lack of Dusky females by an initial mating with females of a closely related subspecies, then backcross the progeny to the Dusky, and so on. This scheme is based upon the assumption that whatever distinctive heritable characteristics the Dusky has will come to predominate in the products of several generations of breeding. In practical terms that means that the more Dusky ancestry the intergrades have, the more they should look like Dusky, with overall dark coloration and heavy streaking on the underparts. This assumption is borne out by the appearance of the intergrades produced in two years of captive breeding, whose ancestry is summarized in Figure 1.

The back, nape, and crown of the Dusky range in overall color from dark chocolate brown to flat black, coming closest to the Fuscous Black or Blackish Brown (1) of Ridgway (1912). (All capitalized color names are those of Ridgway 1912.) The streaked feathers on the underparts are individually about as dark as the back feathers, but because there are fewer of them they look a bit paler and warmer overall, even as pale as Clove Brown. These streaks are sharply defined against a buff-to-white background (Pale Olive-Buff and Light Buff, to nearly White). These streaks are wider (about 2mm) and more abundant on the breast and flanks than on the belly, where they narrow a bit to about 1 mm. They reach posteriorly on the flanks all the way back to the base of the undertail coverts.

The back, nape, and crown of the Scott's Seaside Sparrow appear grayish green overall (Brownish Olive or Citrine Drab, with highlights of Buffy Citrine), though some individuals have substantial amounts of pale reddish brown, such as Sepia or even Chaetura Black. The streaked feathers on the underparts are individually a pale brownish gray (Olive Brown to Chaetura Drab), but as in the Dusky, their sparseness makes them appear paler overall (Deep Mouse Gray to Dark Mouse Gray). The streaks do not have sharp boundaries, and are shorter than those of the Dusky, producing a mottled effect. The streaking appears mainly on the breast, and extends posteriorly only about half as far as in the Dusky.

The foregoing descriptions are based upon study skins at the Florida State Museum. Because we did not want to handle the live intergrades long enough to make the leisurely comparisons possible with skins, we simply described the intergrades from a distance of about 0.3 to 0.5 m as they perched in their aviary. Each characteristic of the intergrades is judged on a scale of 1 to 10, where 1 represents the condition in *peninsulae* and 10 represents that in *nigrescens*.

The 25-percenters are barely distinguishable from Scott's Seaside Sparrows. The contrast of the streaking, and the extent to which it extends posteriorly would each rate no higher than 3. The streaking may be somewhat darker than in *peninsulae*, rating at most a 2. The dorsal coloration does not differ noticeably from Scott's, rating a 1.

The 50-percenters, both F_1 and F_2 , are barely distinguishable from Dusky Seaside Sparrows. The contrast of the ventral streaks with their background rates an 8 or 9, and their posterior extent, at least a 9. The color of the streaks seems a bit paler than in the Dusky, maybe closer to Blackish Brown (3) than Blackish Brown (1). The difference is slight, and this color still rates at least 8. The dorsal coloration, likewise, is perhaps a shade paler than in the Dusky; but it should be considered at least an 8 or 9.

There is little individual variation within each brood of intergrades. None of the described characters in any 25-percenter approaches in rank its corresponding character in any 50-percenter. The immediate impression one gets upon seeing the birds is that the 25-percenters are uniformly darkish gray-green birds with pale mottled breasts, sharply distinguished from all the 50-percenters with their distinct heavy streaking and overall nearly black coloration.

Causes of Mortality

Among the captives, most of the egg failures (failure of an egg to produce a fledgling) consisted of eggs failing to hatch, or deaths of young nestlings. About three-quarters of all nestling mortality occurred when the young were 2 days old or younger. For example, the first nest in Aviary F contained four intact eggs on the 12th day of incubation, but the next day contained only two young. The two progeny that disappeared had presumably just hatched or were attempting to hatch, but had died and were removed by the parents. Adults do not normally remove intact eggs.

This early brood reduction was not common in the nests at Cedar Key, where most mortality was attributable to flooding and predators, mainly Fish Crows

(*Corvus ossifragus*) (see Post et al., this symposium). Out of 110 eggs that failed to produce fledglings at Cedar Key, only two failed to hatch, and there were no cases of early brood reduction similar to that described for Aviary F.

For the captives, we have no satisfactory explanation for losses during the hatching and early nestling periods. Two possibilities are suggested by analogy to the behavior of Seaside Sparrows in the wild.

Disturbance by humans might interrupt or cause premature cessation of incubation, resulting in the failure of some eggs to hatch. We know of only one situation in the wild that causes hatching failures of the sort seen in the aviaries. Incubation usually starts with the laying of the penultimate egg. When male Seaside Sparrows in New York salt marshes were experimentally removed from their territories, the incubating females left the nest earlier than usual to gather food for the young that hatched first, and the hatching rate of the remaining eggs decreased (Greenlaw and Post, unpubl. data). Perhaps this effect could be duplicated in aviaries if females were frightened from their nests by nearby people, and if the hatching of a few eggs reduced the urge to sit tightly to the point at which their fear of humans outbalanced it.

In one nesting the presence of begging juveniles from the previous brood may have contributed to the deaths of small nestlings. This may have resulted from their harassing the female on the nest, interfering with the parents' foraging, or intercepting food being brought to the nestlings. In the wild, the male breeder drives the young from the territory about the time at which the next brood hatches, so that these problems are avoided. In only one captive nesting (data for Santa Fe Teaching Zoo not available) were fledglings still present at the same time as nestlings of the next brood. In Aviary F the two fledglings of the first brood remained in the aviary until 12 June. On 8 June the three eggs in the next clutch were still being incubated. On 9 June the nest contained one nestling and no eggs. In four other nestings, however, early brood reduction occurred when there were no fledglings produced from the previous brood (D1, F1, F4) or when the fledglings had been removed prior to hatching of the subsequent clutch (F3). Since there were other causes of egg and nestling loss (desertion, predation), the total mortality attributable to juvenile interference must be rather small; but future breeders of Seaside Sparrows should keep this possible problem in mind.

If the young remain in the aviary at close quarters with their parents, especially past the hatching of the next clutch, the male breeder may attack or harass them. This may have occurred in the two first broods of 1981. All four fledglings of these two first broods were missing or known dead within a month of their hatching. They were strong fliers, looked healthy, and seemed to be getting plenty to eat. We noticed the male breeder of Pair 6 chasing a juvenile several times but saw no actual attacks. The young of this pair's subsequent brood hatched on 31 May, and this juvenile was last seen alive on 2 June. We found it dead on 4 June. Perhaps the stress of harassment contributed to its death. It had no external wounds.

The other two major problems, accidents and predation, both resulted from defects in aviary design. All

of the aviaries were set directly on the ground without any barrier underlying the earthen floor. Consequently, Norway Rats (*Rattus norvegicus*) burrowed into the aviaries from below, and in at least some cases Yellow Rat Snakes (*Elaphe obsoleta*) found their way in, probably by following these burrows or those of moles. Rats were probably directly responsible for at least one death: In Aviary H we found the incubating female in pieces on her empty nest. Within 2 days after that, the clutch in Aviary G disappeared, as well as the males of Aviaries G and H; either rats or snakes may have been responsible. In 1979 we found a captive Scott's Seaside Sparrow in the stomach of a Yellow Rat Snake. These snakes were probably responsible for the disappearance of at least two other adult Seaside Sparrows that year, and of one clutch of eggs in 1980. In 1981 a Yellow Rat Snake was even found among the Dusks inside the center hexagonal aviary at the Game Commission, but no birds were eaten. Thus neither the nylon-cloth predator baffles nor those of sheet metal worked as we had intended.

Seaside Sparrows have a penchant for working their way into narrow crannies from which they cannot escape. We folded the plastic mesh covering aviaries and partitions in many places in order to make it fit. One Dusky Seaside Sparrow became wedged into one of these folds and died there. A fledgling intergrade tried to hide from us in a fold and became so firmly stuck that we had to dismantle part of the aviary to remove it. The indoor aviary in which we now keep our intergrades of 1981 had a long space between one wooden beam and the mesh, wide at one end and narrowing to nothing at the other. One of the 25-percenters flew into the wide end of this space and worked itself toward the narrow end until it was so tightly stuck it couldn't move. We found it flattened and dead there, and while we looked at the corpse another of the intergrades flew into the same space and became stuck. We rescued it and sealed the space.

Only luck prevented two other inadequacies in aviary design from causing even more losses. First, the plastic mesh with which they were constructed was not protected from mechanical damage. In one case, a feral cat ripped a hole in the top of an aviary; in another, a tree limb ripped the mesh. The cat didn't get in, and we repaired both tears before any birds escaped. Second, the partition between the two cells of our aviaries at the University of Florida was at first set only about 3 cm into the ground. The male of Aviary G was able to find an entrance under the partition, gaining access to Aviary H, where it rampaged for more than a day before we found it and repaired the partition. Fortunately, this uproar did not cause the female of Aviary H to abandon the clutch she was incubating at the time.

REINTRODUCTION

In preparation for reintroduction, we grouped four juveniles and two adult "tutors" (both wild-caught as juveniles the previous year) in one cage that was 13 m². In an attempt to continue imprinting them on the proper habitat (Wecker 1963), we planted *Spartina bakeri* inside and outside the cage. We grouped the juveniles in order to mimic the way juveniles gather and travel in loose flocks during late summer. After a week of becoming accustomed to one another in this aviary, the

birds were released in the middle of a 90-ha grid in the salt marsh at Cedar Key. These birds were not found on the grid later, and lack of funds kept us from making a wider search for them. Our original plan was to hold the juveniles in cages on the introduction site for 2 weeks, in an attempt to ensure imprinting on the settling area. This was not done because of lack of money. Little is known about the behavior of juvenile animals during the time when site-attachment develops; therefore, in the future greater emphasis must be placed upon the reintroduction phase of captive rearing.

DISCUSSION

All things considered, Seaside Sparrows are fairly easy to breed in captivity. Many expected difficulties did not occur. Food and feeding can be kept rather simple; elaborate diets such as the Lanyon mixture seem not to be needed. On the basis of our small sample, it appears that even extreme inbreeding (the brother-sister pair), or crossing with another subspecies does not reduce captive productivity. The F₁ hybrids are as fertile as individuals of "pure" ancestry. Seaside Sparrow pairs seem to breed equally well whether clumped or isolated. Hand-raised birds breed as proficiently as do wild-caught birds or those raised by their parents in captivity. Most breeders renested promptly despite the limited number of nest sites in their aviaries. Only one pair, in 1980, failed entirely to nest; this may be because its aviary, the smallest of all those tried, was too small.

The biggest identifiable problems are predation and accidents, both resulting from improper design of aviaries. Our advice to the Seaside Sparrow aviculturist is to assume constantly that the worst and most improbable disasters are waiting to happen, and to plan accordingly. The Seaside Sparrows should be housed the way a jail warden would house an ingenious and deranged criminal determined to commit suicide. Seaside Sparrows can enter extremely small crevices. No crannies, folds, or other tight spaces can be left in the aviaries. It's best to keep pairs in completely separate aviaries. If aviaries are separated only by partitions, these should be sunk into the ground at least 20 cm. Only 1/4-inch-mesh hardware cloth (or its equivalent in strength and mesh size) should be used as aviary covering. Predator baffles of nylon or sheet metal, even if sunk 1 m in the ground, will not keep out burrowing mammals. If we were to build new Seaside Sparrow aviaries today, they would have some sort of completely enclosed floor, either heavy-gauge hardware cloth (which would still corrode, especially if salt were used in the aviary) or concrete with drainage holes no bigger than about 1/4 inch (ca 6 mm). A layer of soil with marsh plants could be placed over this concrete barrier.

Once the Seaside Sparrows have been protected from predators and accidents, it may be possible to increase further the number of young produced in captivity, depending upon the time, money, and patience available. To begin with, there is the advantage that the breeding season of the captives is long, and that they will renest as many as three times per breeding season. If the number of nestings is limited by the length of the breeding season, then renesting beyond this number might be induced by removing nestlings and hand raising them, or raising them with foster parents. Clutch size might be max-

imized by providing the breeders with an abundance of live food before egg laying. The hatching rate might be maximized by reducing disturbance of incubating females, and perhaps by removing eggs and incubating them artificially or by foster parents. If food is abundantly provided in a conspicuous central location (for instance, by putting live food in an aquarium from which it can't escape), females may well be able to raise their young by themselves, so that each male Dusky can be mated to more than one female per breeding season.

By now we have arrived at a method for breeding Seaside Sparrows of two subspecies in captivity and producing satisfactory numbers of offspring; we have suggested a few ways in which even more young can be produced. These methods will be of value whether the breeding is done entirely with Dusky or with mixed pairs.

We have also learned enough so that we can better compare the biological (as opposed to the legal or financial) merits of the various proposals for saving the Dusky than was possible even a year ago.

Essentially there are two schools of thought about how best to save the Dusky. Both methods, whether employing stored sperm or not, require captive breeding. One prefers to begin immediately with a backcrossing program, to use as much as possible of the Dusky's remaining reproductive lifetime, as a hedge against the possibility that no Dusky females will be found. The other approach is to forego, for at least a while, any crossbreeding with females of another subspecies, in hopes that the real article will show up—in essence, gambling what we now have (live Dusky males) against the hope of something better (Dusky males *and* females).

Both approaches, of course, would involve many of the same practical problems of aviculture, such as those described in this paper: avoiding predation, circumventing brood reduction, and, most importantly, successful reintroduction to the wild. Each approach has some additional problems unique to it.

The chief objection to the all-Dusky approach is its innate uncertainty: There may never be any material with which to start a breeding program, and in the meantime we will be losing the only tangible material we have to work with.

There are four main objections to the backcrossing scheme. The ones we discuss here are not straw men raised by us; they are the ones raised from time to time by various U.S. Fish and Wildlife Service officials as the reasons for that agency's refusal to allow the Dusky to be used in any backcrossing program.

- (1) Perhaps the intergrades will not be fertile. As we have shown, all evidence that exists so far indicates that the F_1 intergrades, even when extremely inbred, are fertile.
- (2) Perhaps the intergrades will never really resemble Dusky. As described in this paper, the F_1 and F_2 intergrades and backcrosses do indeed look like Dusky, in proportion to the amount of their Dusky ancestry. In fact, the 50-percenters look so much like Dusky that it may well take only two or three generations of backcrossing, rather than the usually cited six, to produce offspring indistinguishable from Dusky.

- (3) An initial crossing with Scott's Seaside Sparrow, even if followed by many backcrosses to the Dusky, will dilute the Dusky gene pool. This is a more abstract variant of the former objection, and overlaps with the legal objections to backcrossing. In its biological, as opposed to its legal, form, the objection can be discussed in three ways:

- (a) In the strictest sense, of course the Dusky gene pool consists of the Dusky themselves. No matter how many times they mate with females of other subspecies, they will remain as much Dusky as they ever were. If female Dusky are found, the males, if still alive, will be available, undiluted, to breed with them.

- (b) What would be diluted would be the genotypes of the intergrade progeny, but theirs is not that of the Dusky and the two can be considered to be quite distinct. The hybrid breeding program has always been considered a last-ditch alternative; everyone prefers breeding pure Dusky, but those who favor backcrossing advocate it because it appears very unlikely that any female Dusky will be found. At any rate, for the hybrid breeding program to be available as a back-up measure, the breeding must be done now, while the Dusky are still alive; but the intergrade progeny do not have to be released into the wild until we are sure that there is no hope for the preferred alternative. Thus the creation of an intergrade gene pool does not have to occur in such a way as to foreclose any efforts to find and breed real Dusky. There is no biological reason for the two programs to be mutually exclusive.

- (c) Finally, and most difficult to discuss, is the extent to which the total Dusky-intergrade genotype in the wild would be diluted, in comparison to the natural variation that occurs in any population of animals in the wild. The criteria by which the degree of dilution is to be judged are vague. It is not clear just what characteristics of the Dusky, other than the visible ones already mentioned, are to be protected from dilution, because we know nothing about the Dusky's genotype as such (e.g. how many genes of the Dusky differ from those of other subspecies, what they code for, and how they are distributed among the chromosomes). This is not to say that there are no such characteristics, invisible or unnoticed, that also help to make the Dusky special. In contrast to these doubts, however, the evidence presented in this paper convinces us that the *known* Dusky traits can be preserved (i.e. not "diluted") through backcrossing. Therefore the logical upshot of the all-Dusky school of thought is that it is better to risk the Dusky's known distinctive traits on behalf of the unknown ones, whereas the backcrossing school is willing to risk the unknown ones on behalf of those that are known. So the two factions represent, in effect, champions of two different parts of the Dusky Seaside Sparrow.

- (4) Perhaps the intergrades will not accept the Dusky's habitat when they are reintroduced into the wild. This is really a special case of the general problem of getting *any* captive-bred Seaside Sparrow.

"pure" or intergrades, to live and breed in the Dusky's former habitat. Scott's Seaside Sparrows, F₁ intergrades, and a Dusky all nested in our facsimile Cordgrass marshes in captivity, and we see no reason why backcrosses would have any more difficulty adjusting to the Dusky's habitat than would pure Dusky's.

These things seem clear to us: (1) the known unique traits of the Dusky can be preserved through backcrossing; (2) backcrossing and the search for female Dusky's need not be mutually exclusive; (3) as the male Dusky's age, the need to take advantage of their remaining reproductive lifetime becomes urgent; (4) as time passes, it becomes less likely that female Dusky's will be found; and (5) as we learn more about captive breeding of intergrade Seaside Sparrows, the less the backcrossing option becomes the one about which there are so conspicuously many unanswered questions.

It may not be possible to describe the exact point at which one proposal becomes more biologically realistic than the other, but we have come to the conclusion that the passage of time can only strengthen the argument for preserving the Dusky's known traits through backcrossing, while weakening the case for continuing to hold the Dusky's in isolation.

POSTSCRIPT

As this paper goes to press the Acting Director of the U.S. Fish and Wildlife Service has given provisional approval for the five male Dusky's to be used in a backcrossing program. However, the final plans have yet to be approved by a district office of the USFWS, and there is no guarantee that permission will be given to release the backcross progeny on a U.S. Wildlife Refuge. This postscript may itself be outdated by the time this paper is published.

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Seaside Sparrow Sperm Preservation

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Historically, Seaside Sparrows (*Ammospiza maritima*) have been distributed in the nesting season from Massachusetts to Florida and on the Gulf Coast to Corpus Christi, Texas. All nine subspecies have declined in recent times because of destruction of their primary habitat, the coastal marshes. At least one population—the Smyrna Seaside, *A. m. pelonota*—recently may have become extinct or very nearly so (Herbert W. Kale II, pers. comm.), and another—the Dusky Seaside, *A. m. nigrescens*—is on the verge of extinction. Five surviving Dusky males are being housed at the Santa Fe Teaching Zoo, Gainesville, Florida. We hope that techniques developed in this study may be used for preserving semen from these males.

A rapid, simple, and safe method for semen collection, however, is needed before semen can be preserved. Artificial insemination (AI) in birds is one of many new techniques developed to support captive propagation of nondomestic animals. The massage technique for collecting semen was developed first for domestic poultry (Quinn and Burrows 1936), and has been modified since to adapt it to use with many other species of birds (Gee and Temple 1978). Small quantities of semen can be obtained from many passerines by applying pressure to the cloacal protuberance (Salt 1954, Wolfson 1952 and 1960).

Two other methods of semen collection can be used: electroejaculation and the cooperative technique. Electroejaculation has been successful with ducks (Watanabe 1957), but is not used with other species. The cooperative technique has been used more extensively with raptors because these birds are strongly imprinted on their caretakers (Gee and Temple 1978).

METHODS

Housing

Twelve (8 females, 4 males) Seaside Sparrows (*A. m. maritima*), mist-netted in eastern Maryland in the fall of 1980, were transported to the Patuxent Wildlife Research Center and placed in two covered flight cages with out-

side runs for use during the temperate months. An additional 12 males were added to the colony in July of 1981, but housed in individual cages to reduce intraspecific aggression during the breeding season. The outside runs were planted in April of 1981 with *Spartina alterniflora*, the preferred nesting grass for this subspecies (Post 1974). Two large clumps of native grasses and nest-support structures were added to the outside runs because newly planted *Spartina* would be too sparse to support nesting during the first summer. The males housed in open runs were manipulated for semen only during June to reduce disturbance to the females in their pens. The males housed in individual pens were manipulated for semen from the time of capture until semen production ceased.

Because the House Sparrow (*Passer domesticus*) produces a semen similar in volume and consistency to that of the Seaside, House Sparrows were captured as needed for use as research surrogates. Preliminary studies with the House Sparrows were used, therefore, in developing semen collection and handling techniques for the Seasides.

Semen Collection

An assistant held the Seaside Sparrow in the palm of one hand so the operator could collect the semen. The bird was upright, head toward the assistant, legs between the fingers of the hand and wings restrained by the fourth and fifth fingers of the same hand. The thumb, index finger, and sometimes third finger remained open, exposing the bird's tail and abdomen. The operator stroked the back gently with the thumb and index finger on the left hand, several times from the postdorsal region to the interpelvic tail region, and then to the postlateral region below the tail. Next, the dorsal-lateral surface of the cloacal protuberance was grasped by the thumb and index finger and squeezed in a downward motion, with a repeated increase in pressure, until the semen appeared on the inner surface of the dorsal lip of the vent. The squeezing pressure spreads the lips of the cloaca.

Small cups, beveled-edged slides, and suction devices were used to collect semen. The technique most used was a suction device, a modified white-cell diluting pipette attached to a propipette. This system was used to collect fresh undiluted and diluted semen samples. For a diluted sample, the pipette was filled with a small sample of avian diluent (a solution having the same pH and osmolality as semen) before collecting the semen to prevent drying (the 1:1 semen dilution adjusted by adding the appropriate volume of diluent after collection). Because of the low volume per ejaculate, samples from several birds were pooled for analysis; samples collected with diluent were not used to determine semen pH and osmolality.

Semen Analysis and Freezing

Osmolality of Seaside semen was determined with a Wescor[®] 5100B Vapor Pressure Osmometer^{1, 2} after standardization of the instrument. The vapor pressure osmometer was chosen because of the small sample required (5 μ l) to determine osmolality. The pH of the semen was determined with pHhydrion Papers³. Sperm morphological assessments were made using standard light microscopy techniques.

Semen samples were examined for sperm motility and live-dead smears of most semen samples were prepared using a 5% eosin-10% nigrosin stain. The eosin (red) stain penetrates the dead cell membrane, but not the living cell membrane, and nigrosin (black) provides a dark background on the slide, outlining the living cell.

Preliminary freezing tests with the cryoprotectant, dimethylsulfoxide (DMSO), were conducted using an avian diluent (Sexton 1977) with a pH of 7.0 and an osmolality of 308 mOs. The freezing procedure used in this work was described by Gee and Sexton (1978) for the crane.

RESULTS AND DISCUSSION

Growth of *Spartina alterniflora* in the outside runs was rapid; however, the stand was new and did not attain the density typical of a naturally established stand. Although the females failed to nest, the males produced semen. Also, a few semen samples were collected from the males captured in July, but due to disturbance from the capture, transport, and quarantine, the birds stopped producing semen within 7 to 10 days.

The hand-held position of the bird for semen collection was acceptable and the bird sat comfortably in the hand after the first few attempts at semen collection. Nevertheless, most of the bird was covered by the assistant's hand and the operator had very little room to collect the semen. A holding device that exposes more of the bird's body is under consideration, but the hand-held position is still superior to any others tested.

The small semen volumes (10 μ l or less) were easily recognized but difficult to collect because of the thick, pasty consistency of the samples. The semen had a chalk-white appearance, similar to, but distinctly different from, urates. The small semen volume and pasty consistency

often caused the semen to dry on or in the collecting devices before it could be sealed or otherwise protected from evaporation. Because of complications from drying and from contamination, many pooled undiluted samples had to be discarded. A much greater percentage of useful samples was collected when diluent was in the pipette before collecting the semen. Of four satisfactorily pooled samples collected (relatively clean of wastes with little sign of drying), semen osmolality averaged 348 ± 65 mOs. There were substantial differences between samples (range 249 - 423 mOs) due in part, at least, to fluid and/or contamination. The osmolality of the cleanest sample collected was 334 mOs.

Three samples were used to determine pH, which ranged from 6.0 to 6.4. Even the pH paper required more sample than was available after osmolality testing.

An examination of the semen smears revealed three distinct cell classes—live, dead, and dead-incomplete cells. Cell variation within the three classes included broken tails, missing helical membrane, bent head pieces, collapsed head portions, and missing portions of the anterior head piece. Although the eosin-nigrosin stain is an acceptable procedure to distinguish live from dead cells, it is not a good differential staining method to distinguish cell component parts. For some reason the posterior portion of the head did not stain red in live or dead cells. This part of the cell could be the nucleus, mid-piece, or both. Because it is located between the tail and the anterior portion of the head, it is referred to as the mid-piece. McFarlane (1963) describes this area as the nucleus-mid-piece in sperm of the Passeriformes: Myrtle Warbler (*Dendroica coronata*), Pine Siskin (*Spinus pinus*), and Red-eyed Vireo (*Vireo olivaceus*). In the sauropsid sperm cells of the crane, the nucleus is the major component of the sperm head, whereas the acrosomal cap and mid-piece are small, morphologically distinct parts (Sharlin et al. 1979).

Measurements from the normal, live Seaside Sparrow sperm were $218.1 \pm 4.1\mu$ long, the head was $18.1 \pm 1.7\mu$ long (the mid-piece, included in the head measurement was $6.2 \pm 1.9\mu$ long) and the tail $199.0 \pm 2.7\mu$ long. The ribbon-like membrane appeared to extend from the tip of the cell to within 10μ of the tip of the tail. Exact measurements of the naked tip of the tail were difficult (the naked tip is very fine and it is difficult to distinguish between the broken and the unbroken end). The ratio between the tail length and the head length of the Seaside Sparrow sperm is 11:1, in the middle range of all Passeriformes examined by McFarlane (1963).

Two major types of dead (abnormal) cells were observed, ones missing two-thirds of the head portion and those with an intact head, but usually with a collapsed or shrunken anterior portion of the head. Few dead cells appeared in the normal configuration typical of the normal live cell. Dead cells appeared to be 1.5 to 2 times wider than the live cells, with less twist in the head of the intact cell (usually two complete turns vs. three in the live cell), and the head appeared to be shorter.

Although the number of good semen samples was limited, enough information was gathered to begin altering the standard avian diluent to support sparrow semen. The modified diluent was similar to the avian diluent, but the pH and osmolality were adjusted, 7.0 pH and 308 mOs. A few semen samples from the House

¹ Use of trade names does not imply endorsement of commercial products by the federal government.

² Wescor, Inc. 459 Main, Logan, Utah 84321.

³ Micro Essential Laboratory, Brooklyn, New York 11210.

Sparrow were diluted and frozen. In one sample, about 40% of the sperm were alive before freezing, and nearly 15% of these survived in the sample when thawed 7 weeks later. These percentages compare poorly to the results we have experienced with crane samples (90% live prefreeze and 50% live after thawing), but are typical of results in the early stages of our efforts to freeze crane samples (Sexton and Gee 1978). Under microscopic examination, live cells from the frozen-thawed samples appear to be normal with an intact helical membrane on the head and tail portion of the cell. Since this is the first avian sperm ever frozen with the elaborate helical morphology and exterior ribbon membrane, it was encouraging to find that freezing did not destroy the cell's morphology.

In an attempt to accelerate the sparrow semen preservation study, the birds are now housed in an environmentally controlled facility and, through photoperiod manipulation, should be in semen production later this fall. At that time, semen preservation studies will resume. The cryoprotectant level, dilution rates, and other pre-freeze parameters will be tested for their effects on semen characteristics. To consider the technique successful, we must recover a large percentage of motile cells from the frozen-thawed sample, and inseminate a sufficient number of viable sperm into the females to yield healthy offspring. We hope the technique that is applicable to one species will be applicable to other species in the same genus.

There is little doubt that the decline in coastal marsh habitat of the Seaside Sparrow will continue and population size for several subspecies will shrink. A small population, less than 500 birds (Soulé 1980, Senner 1980; Franklin 1980), leads to a loss of the genetic diversity that has proven essential to the survival of a species. Frozen semen samples, representative of the original population, can be used for insemination many generations later to reestablish genetic diversity and add vitality to less vigorous subpopulations. This technique, in conjunction with habitat protection, may be instrumental in reversing the decline of the Seaside Sparrow.

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Summary of the Seaside Sparrow Symposium

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I'm glad Jim Parnell mentioned my being editor of *The Chat* because I want to begin my comments with a little story about that. When I became editor of *Chat* some 18 years ago, Tom Quay telephoned me and this is what he said: "Eloise Potter, whoever you are, congratulations on your new job. If there is any way my students and I can help you, just let me know." Then, with what I later learned to be typical Tom Quay hyperbole, he added, "This job is going to make you famous!" Looking at my unwashed laundry, my unwashed dishes, and my four partly unwashed children, I laughed and wondered how anyone could think that a volunteer job as editor of a small quarterly magazine about birds could make me famous. But I guess Tom was right after all. Why else would I be standing here right now trying to figure out how to summarize the experiences shared by this distinguished group of scholars yesterday and today? I feel greatly honored by the invitation to participate in this truly useful meeting. Is there anyone here who has not gained a new insight into the biology of the Seaside Sparrow, or has not gained new friends? I have gained both, and I believe most of you have, too.

Tom Quay was the first of many professional biologists to join what I sometimes refer to as the "faculty" of my "private graduate school." When I ask for help with research, writing, and editing, I always find people like Oliver Austin, Jim Parnell, John Funderburg, Dave Lee, and Chan Robbins to be generous with their time and knowledge. They are equally considerate of many other amateurs and young professionals who need advice and guidance. They respect anyone who has a genuine desire to learn more about birds.

A genuine desire to learn more about birds. That is what brought us together to explore the world of the Seaside Sparrow . . . its history, habitat, biology, distribution, vocalizations, behavior, numbers, and management.

What have we learned? First and foremost, there are many things we still do not know about the Seaside

Sparrow even though it is an important indicator species for the estuarine environment. Some papers presented at this meeting raised more questions than they answered. Those were good papers.

The presently recognized races of the Seaside Sparrow are poorly defined. Perhaps we should think in terms of recognizable breeding populations instead of confining ourselves to that term "race." Another point that was brought out is that the breeding and especially the wintering ranges of this species are still poorly known.

The salt-marsh habitat, particularly in estuaries, is fragile and subject to ditching, draining, flooding, filling, pollution, and other modifications related to residential, commercial, and recreational development. Participants in this symposium repeatedly emphasized the decline of the Seaside Sparrow and the need for preservation of large tracts of prime habitat strategically situated throughout the known range. In some places the prime habitat has been destroyed. We must act fast to prevent further major losses.

Although the Smyrna Seaside Sparrow (*A. m. pelonota*) is reported to have been extirpated south of the St. Johns River and the Dusky Seaside Sparrow (*A. m. nigrescens*) is at the very brink of extinction, the Cape Sable Seaside Sparrow—once thought to have been extirpated—has made a remarkable recovery, or at least its population has become better known to us. Sizable breeding populations have been discovered in freshwater habitats in and near Big Cypress Swamp and Everglades National Park, though the race has not been found in recent years at the Cape Sable type locality. We can rejoice in the news that the Cape Sable race and its freshwater habitat appear to be relatively secure.

And finally, various management strategies have been suggested during our sessions. Some of these are highly controversial. We cannot decide here, today, exactly what should be done for the surviving races of the Seaside Sparrow, but we certainly have acquired a

broadened perspective for evaluating the management proposals presented here as well as others that may be suggested in the future.

What is the major accomplishment of this symposium? As important as the formal papers are, I believe the most intense discussions took place informally over coffee and doughnuts or beer and peanuts. Here people were able to clarify misunderstandings and learn to communicate with each other openly in spite of previous differences. Here people were able to explore possibilities they could not appropriately mention in writing in their official capacities. Here the administrative, political, and research people discovered that they have a common interest in preserving salt marshes and in protecting the Seaside Sparrow. The questions of management certainly allow room for honest differences between capable and conscientious biologists. The people who

worked long and hard to make this symposium a reality will feel amply rewarded if those differences have been at least partly reconciled in these two days.

Where do we go from here? Obviously we need to encourage further studies, to investigate courses of action that might benefit the species, and to work together for the preservation of Seaside Sparrow habitat.

The feelings of respect and friendship fostered by this symposium should make it possible for all of us to communicate more effectively in the future than we have in the past and thus to work together for our fascinating avian species—the Seaside Sparrow. It's no Whooping Crane, or Peregrine Falcon, or Eastern Bluebird; but it has, as John Henry Dick so aptly said, a subtle beauty. And it has a unique place in the estuarine environment. Here's to the Seaside Sparrow—long may it sing!



Biographies of Contributors

OLIVER L. AUSTIN JR. is Curator Emeritus in ornithology at the Florida State Museum, Gainesville, Florida. He earned his B.S. at Wesleyan University in 1926 and his Ph.D. at Harvard in 1931. With his father he established the Austin Ornithological Research Station in Wellfleet, Massachusetts, in 1931 and directed its extensive bird-banding operations until 1958. He saw active duty during World War II (Commander, USNR, retired) in the Solomons, New Hebrides, New Caledonia, and New Zealand. He served with the U.S. Military Government in Korea in 1945-1946, and then headed the Wildlife Branch on General MacArthur's SCAP staff in Japan until 1950. He next became editor of the Air Force's survival publications at the Air War College in Montgomery, Alabama, and went to Antarctica as Air Force observer on Operation Deep Freeze I in 1956-1957. He came to the Florida State Museum in 1958. He was Review Editor of *Bird-Banding* from 1951 to 1960 and Editor of *The Auk* from 1968 through 1977. In 1965 he assumed the responsibility for completing the A. C. Bent *Life Histories of North American Birds* series for the Smithsonian. This entailed soliciting material on the family Fringillidae from many contributors, collating and editing it, and filling in the numerous blanks. The Fringillidae *Life Histories* appeared in three volumes in 1968. His publications include *Birds of Newfoundland Labrador* (1932), *Birds of Korea* (1948), *Birds of Japan* (with Nagahisa Kuroda, 1953), *Birds of the World* (1961), *Families of Birds* (1971), and numerous short papers in the periodical literature.

ORON L. BASS JR. is a Wildlife Biologist for the U.S. National Park Service. He received his M.S. from Stephen F. Austin State University, and is on staff at the South Florida Research Center, Everglades National Park, P.O. Box 279, Homestead, Florida 33030. His primary research has concerned the status of endangered and threatened species within the national parks of south Florida. He is a member of the American Ornithologists' Union and Wilson Ornithological Society, serves as Associate Editor of the *Florida Field Naturalist*, and is on the Board of Directors of the Florida Ornithological Society.

ARTHUR W. COOPER attended Colgate University, receiving his B.A. in 1953 and his M.A. in 1955. From there, he went to the University of Michigan where he obtained his Ph.D. in Botany, with a major in Ecology, in 1958. Cooper assumed the position of Assistant Pro-

fessor of Botany at North Carolina State University in Raleigh in the area of plant ecology, and became a full Professor in 1968. While in the Botany Department, Cooper developed, together with graduate students, a research program concentrating on deciduous forests and coastal ecology. During the summers of 1967, 1968, 1969, and 1971 he served as a Visiting Professor at the University of Michigan Biological Station, Pellston, Michigan, where he taught plant ecology. In May 1971, he took leave from N.C. State University to assume the duties of Deputy Director for Programs and Plans of the North Carolina State Department of Conservation and Development. With the reorganization of North Carolina government, he became the Assistant Secretary for Resource Management of the North Carolina Department of Natural and Economic Resources, a position he held while continuing on leave from N.C. State. His duties involved administration of the State's natural resources programs, policy development, and program coordination. In 1976 he returned to N.C. State University as Professor of Forestry and became department head in February 1980. In May 1977, he was appointed as Chairman of the Committee of Scientists for the National Forest Management Act, the committee charged with advising the Secretary of Agriculture as to the adequacy of Forest Service regulations for implementing the National Forest Management Act of 1976. Cooper was elected President of the North Carolina Academy of Science for 1978-1979 and of the Ecological Society of America for 1980-1981. He served as an editor of *Ecology* and *Ecological Monographs* from 1969 to 1978.

MICHAEL F. DELANY is a Wildlife Biologist with the Florida Game and Fresh Water Fish Commission. A native of Connecticut, he obtained his B.S. in Biology from Wesleyan College in 1973. He then taught high school science before continuing his education at the University of Maryland's Appalachian Environmental Laboratory, receiving his M.S. in 1978. Delany's work at the Florida Game and Fresh Water Fish Commission's Wildlife Research Laboratory included participation in the 1980 and 1981 Dusky Seaside Sparrow surveys and the captive maintenance of five of the six known Dusky Seaside Sparrows. His current projects concern the status, distribution, and habitat use of the Florida Grasshopper Sparrow.

JOHN HENRY DICK spent most of his youth at Islip, Long Island, New York, where, at an early age, he became interested in wildlife, particularly raising game birds in captivity. He attended Brooks School in Andover, Massachusetts, and continued his education as a painter at the Yale Art School. Between 1942 and 1946 he was in military service in the Air Corps, with overseas duty in the Pacific theatre. In 1947, he made his home near Charleston, South Carolina, on a thousand-acre plantation where the woods, marsh, and ponds abound in wildlife. He plans to leave Dixie Plantation to the National Audubon Society. Dick's serious painting began in 1947, and since that time he has illustrated *South Carolina Bird Life* (Sprunt and Chamberlain), *The Warblers of America* (Griscom and Sprunt), *A Gathering of Shore Birds* (Henry M. Hall), *Carolina Low Country Impressions* (Sprunt), *World of The Great White Heron* (Marjorie Sanger), and *Birds of Nova Scotia* (Robie Tufts). His interest in photography began in 1956, with the first of eight safaris to Africa, and developed further during trips to Antarctica, the Galapagos, New Guinea, Greenland, the Seychelles, India, Alaska, and Central and South America. In recent years, he has illustrated a guide book, depicting all the birds of India, with a text by Dillon Ripley and Salim Ali, as well as contributing a number of plates to Rudolphe deSchaunsee's *Birds of China*. Dick made his debut as a writer-illustrator with the publication of *Other Edens*, an autobiographical sketch book of his travels. He looks forward to more painting, writing, travel, and photography. He also intends to pursue the breeding of game birds at his plantation, where he has raised to maturity a number of wild species, including 12 Demoiselle Cranes.

JOHN B. FUNDERBURG JR. is a native of Wilmington, North Carolina, where he began developing his skills as a taxidermist during boyhood and later ran a taxidermy business. Following service in the Army Air Force during World War II, Funderburg enrolled at Wilmington College, then transferred to East Carolina University, where he received his B.S. in 1954, following another tour of military service during the Korean conflict. He received his M.S. and Ph.D. degrees from North Carolina State University in 1956 and 1960, respectively. Part of his graduate research involved the Seaside Sparrow. Funderburg taught at NCSU (1956, 1971); Duke University (1959-1960); Florida Southern College, Lakeland, Florida (1960-1971); and Randolph-Macon College, Ashland, Virginia (1971-1974), where he served as Chairman of the Biology Department. He became Director of the North Carolina State Museum in 1974. He serves as Adjunct Professor of Zoology at NCSU and is a member of the Association of Science Museum Directors as well as many other professional and scientific societies.

GEORGE F. GEE obtained his undergraduate degree from the University of Massachusetts in 1960, and his master's degree from the University of Maine in 1962. He completed his doctoral studies at the University of Georgia in 1965, majoring in environmental and reproductive physiology of birds. After 3 years of teaching and research in the Manned Orbiting Laboratory Program (USAF), Gee joined the U.S. Fish and Wildlife

Service as an Animal Physiologist. His research in the Endangered Species Research Program is concerned with environmental and reproductive physiology of captive endangered species and problems associated with their survival in the wild. He is responsible for some teaching and consulting within the Fish and Wildlife Service and with scientists at zoos and universities. Gee's research resulted in the development and implementation of new procedures, some of which have been adopted at other propagation centers. Lighting programs to increase egg production in the Whooping Cranes, Masked Bobwhites, and Aleutian Canada Geese have resulted in increased egg production since the mid-1970s. An artificial insemination program developed in the early 1970s for endangered Whooping and Mississippi Sandhill Cranes is responsible for all their fertile egg production today. Through his efforts and advice he was able to obtain from colleagues, captive propagation of the South American Snail Kite was possible for the first time in 1975. Gene-pool preservation has led to Gee's current research interest in the cryogenic preservation of semen. Since 1977, he and a colleague, Thomas J. Sexton, have developed techniques to preserve semen from the crane, duck, and goose, and they are working on a technique with sparrows.

JON S. GREENLAW is Professor of Biology at Long Island University, C. W. Post Center campus. His undergraduate work for a B.A. was completed in 1963 at the University of Maine. He then entered a doctoral program at Rutgers University in Ecology and Animal Behavior, graduating with a Ph.D. in 1969. His interest in birds developed as he grew up in rural northern Maine. In the past few years, he has worked primarily with North American and Caribbean emberizines. These birds are being used as model systems to explore questions concerning communication, spacing and mating systems, time and energy budgeting, and the evolution of reproductive rates. Most recently, in collaboration with William Post, he has focused on the socioecological bases for the divergent social systems exhibited by *Ammospiza maritima* and *A. caudacuta*. Three papers in this symposium volume are at least partly the result of this work. As an adjunct, long-term project, he also is pursuing an interest in the comparative behavior and systematics of Emberizinae. Illustrative of this interest are the articles on bilateral scratching behavior in ground-feeding birds published in 1976 and 1977 in the *Condor*. Detailed behavioral analyses have been completed or are nearly completed for some members of *Pipilo*, *Ammospiza*, *Melospiza*, and *Zonotrichia*. A manuscript is currently being prepared on the display behavior of *Pipilo erythrophthalmus* that will examine the significance of the behavior in relation to its social system and to other members of the genus.

JOHN WILLIAM HARDY is Curator in Ornithology and Bioacoustics at the Florida State Museum, a position he has held since coming to Florida in 1973. He holds a bachelor's degree from Southern Illinois University (1952), a master's from Michigan State University (1954), and a Ph.D. from the University of Kansas (1959), all in Zoology. After two postdoctoral years, the last at UCLA, he became Director of the Moore Laboratory of Zoology at Occidental College from 1961 until

1973. At Occidental, he continued his predoctoral interests in behavioral ecology of birds, with emphasis on the New World jays, and began to develop his interests in sound recording of bird voices. The Bioacoustics Archive he has established at the Florida State Museum is one of the largest in the country and one of the most important in the world, specializing in Neotropical birds. Hardy's published papers number over 60 and deal with jays, parrots, thrushes, and blackbirds, always emphasizing field study and evolution, including systematics. He first became interested in Seaside Sparrows during his association with David Lee, then an Associate in Natural Sciences in the Florida State Museum. They have long been working on collecting sounds demonstrating geographic variation in song of this species. Hardy's current activities involving the Seaside Sparrow grew out of his association with William Post, who spent the 1979-1981 period as an Adjunct Curator in the Museum at Gainesville, while working on the biology of the Seaside Sparrow.

F. EUGENE HESTER is Deputy Director of the U.S. Fish and Wildlife Service. Born in North Carolina, he received B.S. and M.S. degrees in Wildlife Conservation and Management from N.C. State University and his Ph.D. in Zoology (Fisheries) from Auburn University in 1959. He joined the faculty of the Zoology Department at N.C. State University in 1959, and was leader of the N.C. Cooperative Fishery Research Unit from 1963 until 1971. He was Chief of the Division of Fishery Research (1971-1974) and Associate Director—Research (1974-1981) of the U.S. Fish and Wildlife Service before being appointed to his new position. While on the faculty at N.C. State University, he and his graduate students conducted research on fish genetics. This research of the sunfish family was on phylogenetic relationships as indicated by hybridization success, as well as on selective breeding and heritability of characteristics. Hester also conducted research on the migration and population dynamics of the Wood Duck. By studying nesting progression in 200 nest boxes over a period of several years, and through marking adults by banding and ducklings by web tagging, he and his students were able to gain important insight into nesting and population dynamics. Hester is the author of numerous technical and scientific publications on fish and wildlife subjects, in addition to many popular articles.

HERBERT W. KALE II is Vice-president of Ornithological Research for the Florida Audubon Society. He is a Field Associate of the Florida State Museum, and Adjunct Assistant Professor of Biological Sciences at the University of Central Florida. He received his B.Sc. degree from Rutgers University, and his Master's and Ph.D. degrees from the University of Georgia. Kale's dissertation was on the ecology and bioenergetics of the Long-billed Marsh Wren in Georgia salt marshes, which appeared as Publication No. 5 in the Nuttall Ornithological Club series. Kale is an Elective Member of the American Ornithologists' Union; Editor of *Colonial Waterbirds*, journal of the Colonial Waterbird Group; an Associate Editor of *The Auk*, responsible for editing its Recent Literature Supplement; and is a Florida Region Editor for *American Birds*. He edited the bird volume of the award-winning *Rare and Endangered*

Biota of Florida series. Kale is a member of the Department of Interior's Dusky Seaside Sparrow Recovery Team, and over the past 20 years he has been studying Seaside Sparrow populations in Florida and Georgia. From 1964 until 1975, Kale worked for the Florida Division of Health at the Encephalitis Research Center in Tampa, and at the Florida Medical Entomology Laboratory in Vero Beach, where he was involved in research on vertebrates as potential hosts of mosquitoes and reservoirs of arthropod-borne diseases. Kale's research and conservation interests deal primarily with marsh birds in both coastal and inland areas, beach and roof-nesting Least Terns, and endangered species, particularly the Dusky Seaside Sparrow and the Everglade Kite. His duties with Florida Audubon are primarily concerned with endangered species and habitat conservation.

JAMES A. KUSHLAN is Research Biologist at the South Florida Research Center, National Park Service, P.O. Box 279, Homestead, Florida 33030. He received his Ph.D. from the University of Miami in 1974. His primary research has concerned determining the ecological effects of seasonal hydrologic conditions in tropical marshlands, especially the Everglades, and the study of the status and population dynamics of endangered and threatened species, particularly from the perspective of ecosystem management. He is an Elective Member of the American Ornithologists' Union, Editor of the *Florida Field Naturalist*, and on the editorial board of two journals, *Colonial Waterbirds* and *Wetlands*.

MARY VICTORIA McDONALD, a native of Winchester, Virginia, majored in Biology at Wake Forest University, Winston-Salem, North Carolina, and graduated Cum Laude with a B.A. degree in May 1975. Her master's research began the following fall in the Department of Fisheries and Wildlife Sciences of Virginia Polytechnic Institute and State University. She received her M.S. degree in the summer of 1977 after completing her research project on designing an environmental information system for Virginia counties. The following fall McDonald began teaching in the Department of Life Sciences at Southwest Missouri State University in Springfield, Missouri. During these 2 years in Missouri, she also served as a Chapter President and state Vice-President of the National Audubon Society. McDonald began working on her Ph.D. degree at the University of Florida in the fall of 1979. Her research project is an investigation of the function of vocalizations of Seaside Sparrows. She is a member of Beta Beta Beta, Phi Sigma Xi, Xi Sigma Pi, Phi Kappa Phi, Sigma Xi, the American Ornithologists' Union, and the Wilson Ornithological Society.

THOMAS L. MERRIAM was graduated from the State University of New York at Cortland in 1974 and went on to obtain his master's degree at C. W. Post College, Long Island University in 1979. He received his Ph.D. in entomology from North Carolina State University in 1982. His research interests include medical and veterinary entomology, environmental toxicology, and salt-marsh ecology. He is employed by Union Carbide Agricultural Products Co., Inc., in the Research Triangle Park, North Carolina.

JAMES A. MOSHER received his B.A. degree in 1965 from Syracuse University, his M.S. degree from the State University of New York, College of Forestry (Zoology), and his Ph.D. from Brigham Young University (Zoology) in 1975. His primary area of research is community and population ecology of predatory birds, although he has been actively involved in several other areas of avian research, notably habitat and physiological ecology. He is currently Assistant Professor of Wildlife Ecology with the Appalachian Environmental Laboratory of the University of Maryland. Mosher belongs to several ornithological and ecological societies, Phi Kappa Phi, and Sigma Xi. He is a member of the ICBP's World Working Group on Birds of Prey.

JAMES F. PARNELL, a native of Timmonsville, South Carolina, received B.S., M.S., and Ph.D. degrees from North Carolina State University, with primary training in Wildlife Management, Zoology, and Animal Ecology. He became Assistant Professor at the University of North Carolina at Wilmington in 1964, was promoted to Professor of Biology in 1969 and served as Chairman of the Department of Biology from 1969 through 1971. He became Coordinator of Graduate Studies in Marine Biology in 1981. Parnell's primary research interests are in coastal biology, with major research accomplished in North Carolina on the nesting ecology of waterfowl on the Outer Banks, the habitat relations of warblers in migration, the breeding ecology of colonial waterbirds, the ecology of dredged-material islands, and the breeding biology of Brown Pelicans. Parnell co-chaired two conferences on coastal bird management (1974, 1979) and co-edited the conference proceedings (with Robert F. Soots Jr.). His more than 35 scientific publications on North Carolina bird life include *Birds of the Carolinas* (with Eloise F. Potter and Robert P. Teulings, University of North Carolina Press, 1980), and an *Atlas of Colonial Waterbirds of North Carolina Estuaries* (with Soots, a UNC Sea Grant Publication, 1979). Parnell holds memberships in the American Ornithologists' Union, Wilson Ornithological Society, Ecological Society of America, Wildlife Society, Association of Southeastern Biologists, and North Carolina Academy of Science. He is currently President of the Society of Wetland Scientists.

WILLIAM POST spent his early years on Long Island and in South Carolina. His first publication, at age 16, was a breeding-bird census of a brackish marsh on the north shore of Long Island. After graduating from Harvard, where he studied International Relations, he traveled in Latin America and served in the U.S. Army Reserve. From 1968 through 1972, he studied Zoology at North Carolina State University. Working under John G. Vandenberg, David E. Davis, and Thomas L. Quay, he concentrated in the areas of animal behavior and ecology. His dissertation research involved studies of the evolution of spacing behavior in the Seaside Sparrow. After receiving his Ph.D. in 1972, he became associated with Vandenberg at the Research Division of North Carolina Department of Mental Health. From 1972 to 1975 he worked with Vandenberg in Puerto Rico on the social behavior of Rhesus Macaques. In 1975 he was contracted by the Office of Endangered Species to conduct studies of the Yellow-shouldered Blackbird,

a rare Puerto Rican endemic. Returning to the mainland in 1976, he joined Jon S. Greenlaw at Long Island University, where together they have been studying the evolution of mating systems in Sharp-tailed and Seaside Sparrows. In 1979 Post was contracted by the State of Florida to head a research team to determine ways of saving the Dusky Seaside Sparrow. Post was associated with the Florida State Museum as an Adjunct Associate Curator of Ornithology. He is now conducting research on the Shiny Cowbird in the Caribbean, as a Research Fellow for the University of Colorado. He is also Curator of Birds at The Charleston Museum, Charleston, South Carolina.

THOMAS L. QUAY was born and raised in Mt. Holly, New Jersey. He was graduated from the University of Arkansas in 1938, earned the M.S. degree in 1940 at North Carolina State College, and the Ph.D. degree in 1948 at the University of North Carolina. He was a malariologist in the U.S. Navy 1942-1946, serving in the southwest Pacific and the Philippines. In the summers of 1946 and 1947, he conducted his first Seaside Sparrow and salt-marsh ecology researches, in residence at the Duke University Marine Laboratory at Beaufort, N.C. Quay was a professor of zoology at North Carolina State University from 1948 to his retirement in 1980. He was primarily a teacher—of Ornithology, Ecology, Wildlife, and General Zoology, with research interests in these same fields. He spent his last sabbatical year (1975) on coastal environmental studies, again at the Duke Marine Lab. He plans to continue to publish further, completed researches in his retirement years, working out of his home at 2720 Vanderbilt Avenue in Raleigh. All of Quay's field research on Seaside Sparrows has been conducted in North Carolina, mainly in the Beaufort area, on the nesting populations of *A. m. macgillivraii*; most of this still remains to be published in definitive form. Much of this research has been accomplished with a series of his graduate students: Eugene Hester, James Parnell, William Post, Paul Sykes, Donald McCrimmon, David Adams, John Fussell, Robert Soots, and John Funderburg. "No man is an island."

CHANDLER S. ROBBINS is a Wildlife Biologist in the Section of Migratory Nongame Bird Studies at the Patuxent Wildlife Research Center, Laurel, Maryland. A native of Massachusetts, he received his bachelor's degree from Harvard and his master's from George Washington. Patuxent has been his home base during his 33 years with the U.S. Fish and Wildlife Service, but his field work has taken him to all 50 states as well as to a score of foreign countries. His research has centered on developing methods to inventory and monitor changes in bird populations, and on determining habitat preferences and requirements so that viable management strategies can be developed for enhancing populations of declining avian species. He developed the Breeding Bird Survey program, under which some 1,900 randomly distributed 50-stop roadside routes are covered annually in the United States and Canada to provide information on bird population trends. He is coauthor, with R. E. Stewart, of *Birds of Maryland and the District of Columbia*, and senior author of the Golden Field Guide, *Birds of North America*. He has written more than a hundred scientific papers and an additional 160

short articles on bird distribution, migration, and populations. He has served as Editor of *Maryland Birdlife* for 35 years and as Technical Editor of *Audubon Field Notes* and *American Birds* for 25 years. He represents the United States on the International Bird Census Committee, is secretary of the International Bird Ringing Committee, and is active on committees or boards of several other ornithological and conservation organizations.

THOMAS J. SEXTON is a native of New Jersey. He received his B.S. degree in 1964 from Delaware Valley College and his M.S. degree in 1966 from the University of New Hampshire. Sexton received his Ph.D. from the Pennsylvania State University in 1971. After graduation from Penn State he joined the U.S.D.A., Agricultural Research Service at Beltsville, Maryland, as a Research Physiologist. In 1978, he was appointed Chief of the Avian Physiology Laboratory. Also, he is an Adjunct Associate Professor of Poultry Science at Auburn University. His research program at Beltsville deals with the application of semen preservation techniques to improve male reproductive efficiency. Sexton's mailing address is: Agricultural Research Service, Beltsville Agricultural Research Center, Beltsville, Maryland 20705.

PAUL W. SYKES JR., a native of Norfolk, Virginia, attended the Virginia Polytechnic Institute (1956-1958) and received his B.S. in Forest Management from North Carolina State College in 1961. Commissioned an Ensign in the U.S. Naval Reserve in 1961, he served on active duty from then until 1964. In 1967 he received his M.S. in Zoology from North Carolina State University. His thesis research was on the fall migration of land birds along the Outer Banks of northeastern North Carolina, under the direction of Thomas L. Quay. From 1967 through 1982 Sykes was a Wildlife Biologist (research) for the Southeastern United States in the Endangered Species Research Program of the U.S. Fish and Wildlife Service's Patuxent Wildlife Research Center, Laurel, Maryland, stationed at Delray Beach, Florida. His research has dealt primarily with the Everglade Kite in Florida, but he has also done considerable work on the Bald Eagle, Sandhill Crane, Puerto Rican Parrot, Ivory-billed Woodpecker, Dusky Seaside Sparrow (at Merritt Island, Florida, 1969-1976), Cape Sable Sparrow, bird use of flooded agricultural fields, and bird migration. Memberships include Xi Sigma Pi (Forestry), Phi Sigma Society (Life Science), American Ornithologists' Union, Wilson Ornithological Society, Cooper Ornithological Society, and Northeastern and Eastern Bird-Banding Associations. His more than 70 published articles include "Decline and disappearance of the Dusky Seaside Sparrow from Merritt Island, Florida" (*American Birds* 34:728-737), and Sykes is working on a paper with Willard Leenhouts summarizing 13 years of work on restoration of high salt marsh at Merritt Island, Florida, in what was formerly Dusky Seaside Sparrow habitat. Sykes is presently working at the U.S. Fish and Wildlife Service's Mauna Loa Field Station in Hawaii National Park.

DALE L. TAYLOR was a Fire Ecologist with the National Park Service from 1977 through 1981. As a team leader at the South Florida Research Center,

Everglades National Park, he measured impact of long-term use of prescribed fire on a Slash Pine community, studied fire history in the park, and worked on frequency and season for prescribed fire use on four plant communities within the Park and Big Cypress Preserve. He assisted in developing annual fire management plans for the two parks. After he received his Ph.D. in 1968, the National Geographic Society supported his continuing studies of fire history and fire ecology in Yellowstone National Park. From 1974 through 1977, he did seasonal research on fire ecology and worked on a fire plan for Grand Teton National Park. In all four parks, his work involved impact of fire on birds, small mammals, plant species, and soil nutrients. Taylor holds bachelor and master of science degrees from Kansas State University. He advanced through the academic ranks as a college teacher, specializing in undergraduate teaching at three liberal arts colleges. He served as Head of Biology and Chairman of the Science Division at Sterling College, Kansas, before joining the National Park Service on a permanent basis. He is currently a Fire Ecologist for the Bureau of Land Management, Alaska State Office, where he is co-chairman of the Alaska Land Use Council Fire Management Subcommittee. The Committee is charged with producing interagency fire plans for Alaska.

THOMAS A. WEBBER received his bachelor's degree in Biology from the University of California at Los Angeles, and is now a graduate student in Zoology at the University of Florida. His major scientific interests are the vocalizations and other behavior of birds, especially jays. He has studied several species of communally breeding jays in Mexico with J. W. Hardy of the Florida State Museum, and his dissertation is on the behavior of Scrub Jays (*Aphelocoma coerulescens*) in Florida and California. In early 1981 he found himself unofficial curator of Seaside Sparrows at the Florida State Museum, upon the arrival of the five captive Seaside Sparrows that form the basis of his contribution to this symposium.

HAROLD W. WERNER is the Fish and Wildlife Specialist at Sequoia and Kings Canyon National Parks. Werner attended the University of South Florida from which he received his B.A. and M.A. degrees in Zoology in 1969 and 1976, respectively. Between receiving these degrees, he graduated from the United States Army Aviation School in 1971 and served afterwards in Vietnam as a helicopter pilot. In addition to his present assignment, he worked in Everglades, Carlsbad Caverns, and Guadalupe Mountains National Parks. His positions in resource management have included working with caves, endangered and exotic species, fire, fisheries, water quality, and wildlife.

LOIS A. WOOD graduated with a B.S. from the University of Massachusetts in 1975 and an M.S. from Florida State University in 1979. All of her postgraduate experience has been in field research on endangered species projects in Florida: Dusky Seaside Sparrow, Shaws' Swallowtail Butterfly, Bald Eagle, Red-cockaded Woodpecker, and Gopher Tortoise. She hopes to continue with research that will ultimately counsel policy-making decisions regarding conservation of wildlife and natural resources. Being a member and president of an

organic gardening cooperative, she enjoys a small measure of self-sufficiency maintaining a year-round vegetable supply. Future prospects include earning a doctoral degree in Entomology.

GLEN E. WOOLFENDEN, Professor of Zoology, Department of Biology, University of South Florida, Tampa, Florida 33620, is a native of New Jersey. He received a bachelor's degree from Cornell University (1953), a master's from the University of Kansas (1956), and a Ph.D. from the University of Florida (1960). Woolfenden has published over 80 ornithological papers on a diversity of topics, including osteology, paleontology, molt, distribution, and breeding biology. Since 1969 he has been studying cooperative breeding in birds, based primarily on a long-term demographic study of the Florida Scrub Jay at the Archbold Biological Station, where he is a research associate. He has given numerous invited lectures on cooperative breeding in birds, including the David E. French Lecture of the Claremont Graduate Schools (1978), the Harry Hann Lecture at the University of Michigan Biological Sta-

tion (1976), and the Queen's Quest Lectures at Queen's University, Kingston, Ontario (1982). In 1978 he received the Ernest P. Edwards prize of the Wilson Ornithological Society. For his master's thesis, published in 1956, Woolfenden studied the breeding behavior of sympatric populations of Seaside Sparrows and Sharp-tailed Sparrows in a New Jersey salt marsh. Later he wrote the species account for the nominate race of the Seaside Sparrow for the *Bent Life History* series (1968). Woolfenden is a former vice-president, councilor, and associate editor for the American Ornithologists' Union; current vice-president of the Florida Ornithological Society; and a member of the "Committee of 100" of the International Ornithological Congress. A member of the faculty of the University of South Florida since 1960, he has received the awards of Distinguished Lecturer and Distinguished Teacher from the College of Natural Sciences, and of Outstanding Faculty Researcher from the Society of Sigma Xi. Several students have completed advanced degrees under his direction, including Harold W. Werner, coauthor of the paper on the Cape Sable Sparrow included in these proceedings.



CONTRIBUTIONS OF THE NORTH CAROLINA BIOLOGICAL SURVEY — 1982

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